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Systematics of the Chiropteran Family Mormoopidae

By

James Dale Smith

UNIVERSITY OF KANSAS
LAWRENCE 1972

March 10, 1972

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Miscellaneous Publication No. 56

March 10, 1972

Systematics of the Chiropteran Family Mormoopidae

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University of Kansas
Lawrence
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INTRODUCTION

The mustached bats, naked-backed bats, and ghost-faced bats of the New World family Mormoopidae occur from southern Texas through México and Central America into South America to southern Brasil. Members of this family also are found on the Greater Antilles, some of the islands of the Lesser Antilles, Trinidad, and in the Dutch West Indies. The ecological associations of the included species, although not yet clearly defined, seem to be rather broad; the bats range from humid tropical to semiarid and arid subtropical environments.

Since the discovery of mormoopid bats in the early Nineteenth Century, their taxonomic treatment has been varied and, at times, controversial. Prior to this study, mormoopids, all of which are insectivorous, were generally considered as a distinct subfamily (Chilonycterinae) of the family Phyllostomatidae. However, mormoopids lack a cutaneous nose-leaf like that possessed to some extent by most phyllostomatids; furthermore, the latter are principally frugivorous. In recent years, mormoopids have been grouped in three genera —*Chilonycteris, Pteronotus,* and *Mormoops*—by some authorities, or in two—*Pteronotus* and *Mormoops*—by others.

Mormoopid bats were first reviewed critically by Rehn (1902, 1904a, and 1904b), whose studies were based on 188 specimens. Rehn recognized three genera, eight species, and 14 geographic races. I have had at my disposal more than 5000 specimens; herein I recognize two genera and eight species. Two species are monotypic; six are polytypic and are composed of 21 subspecies, three of which are described as new.

The aims of this study were to collect and correlate as much information as possible concerning the relationships of the Mormoopidae, and to bring into focus some of the problems facing mammalogists with interest in the Neotropical bat fauna. Specifically, the study involved: a systematic revision, primarily concerned with the familial and generic levels; an interpretation of the phylogenetic relationships and evolution of the recognized taxa; a study of variation, both geographic and non-geographic, within species; and a preliminary appraisal of zoogeographic features that have influenced the dispersal and speciation of the group.

MATERIALS AND ACKNOWLEDGMENTS

Most of the 5173 specimens examined were conventionally prepared study skins and skulls. Each specimen usually was accompanied by a label bearing information concerning date and place of capture, sex and frequently data relating to reproductive condition, four standard external measurements, and name of collector. Additional material examined included complete skeletons, skulls unaccompanied by skins or removed from specimens preserved in alcohol, and entire individuals in alcohol.

I am deeply indebted to the following institutions and persons who put this material at my disposal (abbreviations preceding the names of institutions are used throughout the text to identify the source of specimens):

AMNH American Museum of Natural History (Karl F. Koopman)
ANSP Academy of Natural Sciences of Philadelphia (R. R. Grant, Jr.)
ASC Albert Schwartz (private collection)
BMNH British Museum (Natural History) (J. E. Hill)
CAS California Academy of Science (Robert T. Orr)
ENCB Escuela Nacional de Ciencias Biológicas, México D. F. (Ticul Álvarez)
FMNH Field Museum of Natural History (Joseph C. Moore and Philip Hershkovitz)
IB Instituto de Biología, Universidad Nacional Autónoma de México, México (Bernardo Villa-R.)
IZT Instituto de Zoología Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Caracas (Juhani Ojasti and Edgardo Mondolfi)

KU The Museum of Natural History, The University of Kansas (J. Knox Jones, Jr.)
LACM Los Angeles County Museum (Donald Patten and Andrew Starrett)
MCZ Museum of Comparative Zoology, Harvard University (Barbara Lawrence)
MLS Museo de Historia Natural, La Salle, Caracas, Venezuela (Omar Linares)
MPEG Museum Paraense Emilio Goeldi, Belém, Brasil (Fernando C. Novaes)
MSU The Museum, Michigan State University (Rollin H. Baker)
MVZ Museum of Vertebrate Zoology, University of California, Berkeley (Oliver P. Pearson, W. Z. Lidicker, Jr., and Seth B. Benson)
RMNH Rijksmuseum van Naturlijke Historie, Leiden, Netherlands (A. M. Husson)
ROM Royal Ontario Museum (R. L. Peterson and J. R. Tamsitt)
TCWC Texas A and M University, Texas Cooperative Wildlife Research Collection (W. B. Davis and Dilford C. Carter)
UMMZ University of Michigan, Museum of Zoology (E. T. Hooper and W. H. Burt)
USNM United States National Museum, including the Biological Surveys Collection (C. O. Handley, Jr., and R. H. Manville)

I thank the following agencies for grants-in-aid of travel to the major North American mammalogical collections: the Committee on Systematics and Evolutionary Biology (National Science Foundation Program GB-4446X) at The University of Kansas (an 11-month traineeship was also granted by this committee); the Committee on Grants-in-aid of Research, the Society of the Sigma Xi; the Watkins Museum of Natural History Fund, The Museum of Natural History, The University of Kansas; and the Research Awards Committee, Kansas Academy of Science. Furthermore, I thank the Universidad de Oriente, Cumaná, Venezuela, for a research grant to defray the expenses of field investigation and a vehicle during my 18-month stay in Venezuela. Field work that resulted in the collection of some of the material reported herein was made possible by The Kansas University Endowment Association, and by several contracts (DA-49-193-MD-2212, DA-49-193-MD-2788, DA-MD-49-193-62-G54, and DA-MD-49-193-63-G94) from the U.S. Army Medical Research and Development Command.

I am especially grateful to J. Knox Jones, Jr., who guided this research and spent many hours critically reviewing the manuscript. I am also indebted to Karl F. Koopman and William M. Bass, III, who have given a great deal of their time in reviewing the manuscript, and to Terry A. Vaughan for his valuable counsel regarding functional and anatomical aspects of chiropteran flight.

Valuable statistical advice and aid in computer processing were provided by F. James Rohlf and John Kishpaugh, Department of Entomology, The University of Kansas, and Dennis Powers, Royal Ontario Museum, who wrote the computer program (UNIVAR) for obtaining standard statistics, univariate analysis of variance, and sum of squares simultaneous testing procedure, used in this study. I also appreciate assistance by J. E. Hill, British Museum (Natural History), who provided critical information regarding holotypes housed in that institution.

Lastly, I take great pleasure in acknowledging: my parents, Mr. and Mrs. Frank Dale Smith, who encouraged me and made possible the early part of my formal education; my wife, Nancy, who aided me with her patience and typed the manuscript; many of my fellow graduate students who offered useful suggestions; and Mrs. Ruth Fauhl and Miss Gayle Hassler, The University of Kansas Library, for their assistance in obtaining various important references.

METHODS

Cranial measurements were taken with dial calipers, calibrated in twentieths of a millimeter, and were recorded to the nearest tenth of a millimeter. Standard external measurements were copied from specimen labels, but were not used in analyses because of their high degree of variability, as indicated by high coefficients of variation, probably reflecting the variation in measuring techniques

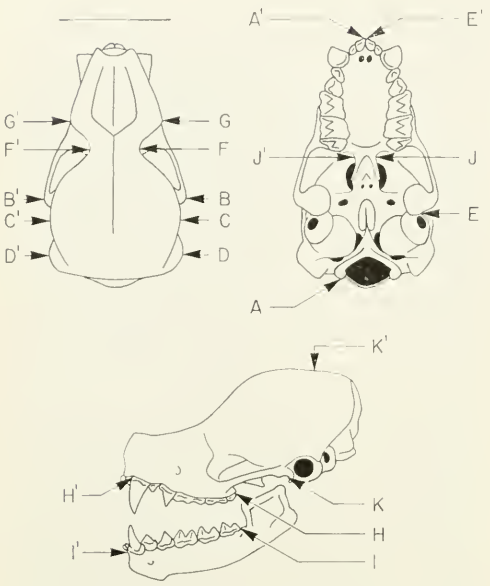


FIGURE 1. Diagrammatic dorsal, ventral, and lateral views of skull of *Pteronotus parnellii* showing measurements used in this study. See text for further explanation of measurement terminology and definition. Line above dorsal view is 10 mm in length.

employed by different collectors (Van Gelder, 1959:239). The length of the forearm (measured with dial calipers on dried skins and selected specimens preserved in alcohol) was taken from the posteriormost projection of the elbow (olecranon process) to the anteriormost projecting part of the wrist joint with the wing in a flexed position. Only adult specimens (phalangeal epiphyses completely fused) were utilized in this study. Skulls not accompanied by skins were considered to be adult if all teeth were fully erupted and the cranium was well ossified.

Cranial measurements employed in this study were selected after preliminary consideration of their variance within and between samples. Most are standard measurements customarily used by chiroptologists, but some are of my own invention owing to the unusual shape of skulls in some mormoopids. All cranial measurements employed are defined below; letters in parentheses refer to figure 1. All measurements given in the text are in millimeters unless otherwise noted.

Condylobasal length (A-A').—Least distance from posteriormost projection of exoccipital condyles to the anteriormost projection of the premaxillae.

Zygomatic breadth (B-B').—Greatest width across zygomatic arches at right angle to longitudinal axis of cranium.

Breadth of braincase (C-C').—Greatest width across the braincase, at right angle to the longitudinal axis of cranium, at point above auditory meatus. This measurement was taken somewhat more posteriorly on *Mormoops* than on *Pteronotus*, owing to the different shape of the skull.

Mastoid breadth (D-D').—Greatest width across mastoidal flanges, at right angle to longitudinal axis of cranium in *Pteronotus*; greatest width across mastoid processes in *Mormoops*, because flanges are not developed in this group.

Zygorostral length (E-E').—This measurement, not easily obtained from skulls of some groups of bats, proved to be a useful dimension of the frontal portion of the skull. In the mormoopid bats, the glenoid fossae are raised above the floor of the basicranium (viewed from below), and are set slightly anterior to and extend above the auditory bullae; this allows for the pointed tip of the calipers to be placed behind the post-glenoid process. The measurement is the least distance between this point and the anteriormost projection of the maxillae.

Interorbital breadth (F-F').—Least width across the interorbital constriction, at right angle to the longitudinal axis of the cranium.

Rostral breadth (G-G').—Greatest width across rostrum, at right angle to longitudinal axis of cranium; this measurement is approximately above the first molars in *Pteronotus* or second premolars in *Mormoops*.

Alveolar length of maxillary toothrow (H-H').—Least distance from posterior lip of alveolus of M3 to the anterior lip of alveolus of canine.

Alveolar length of mandibular toothrow (I-I').—Least distance from posterior lip of alveolus of m3 to anterior lip of alveolus of inner incisors.

Breadth of post-palatal extension (J-J').—Least width across posterior extension of hard palate.

Depth of braincase (K-K').—Due to the position of the glenoid fossae (discussed under zygorostral length) this measurement may be taken directly from the skull without the use of a standardized glass slide, and despite the fact that auditory bullae may be missing or damaged; the calipers must have a relatively thin knife-like blade. To take this dimension, one blade is laid across the glenoid fossae and

the other blade is brought into contact at the desired position—in this study the point of contact was the juncture of the midline and frontal-parietal sutures.

Other quantitative characters used in the generic analysis were 10 cranial angles, CAB, CAE, CAD, ACE, ADE, DEC, IFG, IFH, FIJ, FGJ (Fig. 2). Twenty qualitative, multistate characters, coded non-additively (Sokal and Sneath, 1963: 77), also were employed in this analysis and are as follows: attachment of wing membranes to body; direct or indirect attachment of wing membrane and uropatagium to ankle; ligamentous attachment of wing membrane and uropatagium free or tightly bound to tibia; shape of ear; notch on lateral edge of ear present or absent; tooth-like serrations on antero-medial edge of ear present or absent; extent of fusion of ears on top of muzzle; rostral tubercle present or absent; extent of lip ornamentation; lateral spikes on labio-nasal plate (Fig. 11) present or absent; shape of tragus (Fig. 10); length of dorsal pelage; distinct color bands present or absent on hairs of back; flange on anterior edge of proximal end of the humerus present or absent; second lower premolar long and narrow or round and peg-like; number of lobes on outer lower incisors; degree of concavity of nasal root; heel on upper inner incisors present or absent; degree of bifurcation of upper inner incisors; structure of upper canine.

Preliminary testing of males and females of three species, *Pteronotus personatus, P. davyi,* and *Mormoops megalophylla,* revealed significant secondary sexual variation. Additional study showed that not all characters were thus influenced, nor did the same characters of different species necessarily show significant secondary sexual variation (see discussion beyond). At any rate, during the initial examination and measurement of specimens and the subsequent analyses of geographic variation, males and females were segregated.

Illustrations of skulls and skeletal elements were made by tracings from pho-

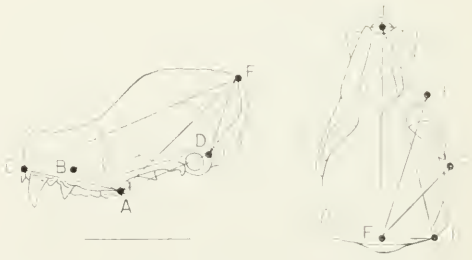


FIGURE 2. Diagrammatic representation on skull of *Pteronotus parnellii* of cranial angles used in the generic analysis section of this study. See text for discussion. Line below lateral view is 10 mm in length.

tographs of known scale or with a Wild Heerbrugg Stereomicroscope fitted with a drawing tube. The cranial angles, mentioned above, also were determined with the aid of this scope. This was accomplished by recording the position of specific anatomical landmarks of the cranium on paper and then measuring the angles by means of a 360-degree protractor. This proved to be a useful technique, but was somewhat time consuming. In addition to measuring cranial angles, cusp positions on molar teeth were examined.

Molt was studied by mapping molt patterns of a number of individuals taken at various times of the year. Data concerning reproductive activity were recorded when present on specimen labels. In those cases where no information was given for a known female, an attempt was made to determine at least whether or not she had been lactating at the time of capture, as judged by the presence of enlarged mammae. Molt data and reproductive information were treated together in order to determine whether the two were correlated. Notations as to color of pelage are for the most part in the vernacular. However, in some cases it was useful to use the color terms of Ridgway (1912); these are capitalized in the text.

In the systematic accounts the genera and subgenera are arranged in phylogenetic order. Within subgenera, the type species is considered first. Likewise,

in the species accounts, the nominate subspecies is considered first, followed by the remaining subspecies arranged from north to south by geographic unit in cases where there are more than two recognized races. The familial and generic synonymies consist of the citation to the original proposal of the recognized name, followed chronologically by other synonyms. Subspecific synonymies consist of the name as originally proposed, followed by the first usage of the name combination here employed, if different from the original name, and any pure synonyms. Wherever necessary, other name combinations are discussed in the remarks section of the accounts of the individual subspecies.

In the lists of specimens examined, countries are listed from north to south, with the Caribbean islands following mainland localities; states, counties, provinces, departments, or parishes are arranged alphabetically; localities are arranged from north to south within political subdivisions. If two localities lie at the same latitude, the westernmost is listed first. Localities in italic type were not plotted on distribution maps because undue crowding of symbols would have resulted. Additional marginal records of note are cited in some accounts.

Statistical analyses.—Statistical analyses used in this study were selected for their utility and ease of interpretation. Discussions and logic of the testing procedures used will be found in Simpson *et al.* (1960), Steel and Torrie (1960), and Sokal and Rolhf (1969). All computations were performed on a GE 635 computor made available to me by the University of Kansas Computation Center through funds allotted to the Department of Zoology.

In the past, some workers have been satisfied simply to calculate means and ranges of samples for the interpretation of variation in mensural data or to use "Dice-squares" or "Dice-grams," which incorporate other valuable parameters, such as standard deviation and standard error of the mean. The Dice-square first was used by Dice and Leraas (1936). These devices have been widely employed, but they have a number of disadvantages. As pointed out by Sokal and Rinkel (1963:473), in the case where a large number of group-means are to be compared (such as in a study of geographic variation), trends are difficult or impossible to follow by means of the Dice-square. When the variation is linear in character or when there are only a few means to be considered, the Dice-square may be applied satisfactorily.

Perhaps the most serious drawback to the Dice-square, is that *t*-tests for pairs of group-means have been erroneously applied to them under the assumption that ordinary levels of significance apply. Sokal and Rinkel (1963:473) pointed out that in such instances the investigator does not take advantage of a pooled variance of all samples and thereby obtains a greater number of degrees of freedom that, in turn, raise the level of significance of the test being applied. Also in this regard, such comparisons do not comply with the random sampling assumptions of the *t*-test in that they are usually conducted *a posteriori* rather than *a priori*. Furthermore, Duncan (1955: 25-26) showed that the protection levels of the *t*-test decrease drastically with each additional comparison beyond two means. Therefore, a two-mean *t*-test may have a protection level of 95.0 per cent, whereas three- and four-mean tests have protection levels of approximately 90.2 and 79.7 per cent, respectively. These levels are so low as to invalidate the use of multiple *t*-tests as satisfactory procedures at the five per cent fiducial level.

For this study, standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) were computed for all samples where geographic variation was of interest, or for both sexes in those instances where secondary sexual variation was studied. Where several group-means were to be compared, a

single classification analysis of variance (univariate ANOVA) was used to test for significant variation within the entire sample of group-means. In this analysis, an F value is computed and checked in an F-table under the appropriate degrees of freedom and the 0.05 level of significance. If the observed F value was greater than the critical F value (from the table), significance differences existed between group-means of the sample, thus warranting further testing. In those cases where only two group-means were tested (for example, comparisons between males and females for secondary sexual variation), no further testing was necessary.

In most cases, significant F values were observed when a number of group-means were compared in an analysis of geographic variation, and it was necessary to continue testing for significant and non-significant differences among these sample means. A wide variety of "multiple comparisons tests" for *a posteriori* comparisons of analysis of variance exists; descriptions of these tests are found in Sokal and Rohlf (1969). Sokal and Rinkel (1963) and Sokal and Thomas (1965) used and discussed one of these, the Student-Newman-Keul multiple comparisons test, in analysis of geographic variation. The multiple comparisons test I used is Gabriel's (1964) Sum of Squares Simultaneous Testing Procedure (SS-STP). The application of the SS-STP to studies of geographic variation is discussed in detail by Gabriel and Sokal (1969). Essentially, the sample means are ranked in order of decreasing magnitude and beginning with the first mean, sums of squares are calculated by sequentially adding subsequent sample means until a maximal non-significant "subset" of means is determined. This process is repeated beginning with the second sample mean and proceeding until all non-significant subsets are determined. The determination of maximal non-significant subsets is accomplished by using a single variance—the pooled, within group or error mean square—obtained from the initial analysis of variance. An addition to the advantage of subset determination by a single variance is that in the SS-STP analysis the probability of making a *type I* error (rejection of a null hypothesis that is, in fact, true) is determined by an experiment-wise error rate, which in turn reflects the probability level of the selected "critical" F value (0.05 level, in this study).

Gabriel and Sokal (1969) suggested that only samples from contiguous locations should be considered in calculating maximal subsets of sample means; contiguity being judged by geographic closeness. Such a system reduces the number of comparisons and perhaps gives a more precise picture of the geographic variation. While comparisons of locality means from, say, Sinaloa, México, with those of Tingo María, Perú (certainly non-contiguous localities), may not be particularly informative, many systematically valid and interesting comparisons can be made between localities that are not contiguous. Overall locality comparisons in this study yielded a certain amount of information concerning trends and effects in insular and peninsular regions.

As yet, no satisfactory method of illustrating the results of the SS-STP has been developed. Usually, localities representing the various sample means are plotted on a map, and each is identified in some way with its respective mean, which appears in an array of means located to one side of the map. In this array, means are arranged in order of decreasing magnitude from largest to smallest and maximal non-significant subsets of means are delineated by a line that connects all means within a single non-significant subset (Fig. 19). Such an illustration allows the reader to see which groups of sample means are "clustered" and significantly different from which other groups. However, as the number of sample means (localities) and widely overlapping subsets increases, the clarity of the illustration tends to decrease. Of

course, the easiest situation to interpret is the occurrence of non-overlapping subsets. In addition, there are problems involved in the correlation and comprehension of several (in this study 12) of these SS-STP results simultaneously. Because a particular locality may exhibit different subset relationships in different characters, it would be desirable to be able to determine the overall relationships between localities based on all characters examined.

Gabriel (1967) developed a simultaneous testing procedure for a multivariate analysis of variance (MANOVA), and a program (MULDIS) is available in the Numerical Taxonomy System from the Computation Center at the University of Kansas. However, neither of these procedures was used because of problems relating to missing data. Instead, I employed another package program (CLNST-Version 2) also available in the Numerical Taxonomy System at Kansas. Among other things, this program computes a matrix of Pearson's product-moment correlations and a matrix of taxonomic distance coefficients from standardized character values. Additionally, cluster analyses using UPGMA (unweighted pair group method using arithmetic averages) are performed on the correlation and distance matrices and a phenogram is generated for each. These phenograms are next compared with their respective matrices, and a coefficient of cophenetic correlation (Sokal and Sneath, 1963) is computed for each comparison. These matrices and their respective phenograms may be used to interpret the overall similarities between OTUs (standardized locality means in the case of geographic variation). I employed the distance matrix and distance phenogram rather than the correlation matrix and phenogram, because the cophenetic correlations were higher for the former. Computation and discussion of the distance coefficient can be found in Sokal (1961), Sokal and Sneath (1963), and Proctor (1966).

This same set of programs also was used in the analyzing the generic classification of mormoopid bats. In addition, a matrix of correlations among characters and a matrix of the first three principal components based on correlation among characters were computed. Projections of OTUs onto these principal components also were computed and three-dimensional models were drawn with a Benson-Lehner incremental plotter from a tape prepared from the projection and distance matrices (Rohlf, 1967, 1968).

HISTORICAL REVIEW

The taxonomic history of the family Mormoopidae began in 1821 when William Elford Leach described *Aello* and *Mormoops*. It is appropriate to point out that in Leach's time the classification of bats, as well as that of mammals in general, was in a state of uncertainty and disagreement. Nearly every prominent taxonomist from the post-Linnaean period of the Eighteenth Century to the mid-Nineteenth Century presented, at one time or another, his own conception of the natural arrangement of mammals. For the most part, no two classifications were alike or even comparable. In the following discussion, the original orthography is preserved in appropriate places for historical reasons and ease of discussion.

Early in the formative period of chiropteran classification, the mormoopid bats were variously allied with the Noctilionidae and Phyllostomatidae, both families having somewhat broader limits than as currently defined. Because the mormoopids seem to be more closely related to these two families than to any other New World assemblage, I have attempted in the following discussion to maintain the Noctilionidae and Phyllostomatidae in proper perspective with the Mormoopidae.

Gray (1821) divided the bats into two orders (Fructivorae and Insectivorae) in the class Cheiroptera. He divided the Insectivorae into two fami-

lies (Noctilionidae and Vespertilionidae) and further subdivided the former into three "Races" based primarily on characteristics of the nose—nose simple, nose warty, or nose appendaged. The presence or absence of appendages on the nose also seems to have influenced Leach. In the family Vespertilionidae, under the heading *Rhinophyllis nullis* (bats without foliaceous nose appendages), Leach (1821a:69) named the genus *Aello*. Within the same family, but under the heading *Rhinophyllis instructae* (bats with foliaceous nose appendages), Leach (1821b:74) established the genus *Mormoops*. Neither of these genera appeared within the context of a general classification until Gray (1825:338) mentioned the genus *Mormoops* in an arrangement that contained all bats in one family—Vespertilionidae. This family was placed in the order Primates and was further divided into five tribes, two of which possessed nose-leaves and were designated *Rhinolophina* and *Phyllostomata*. The genus *Mormoops* was assigned to the *Rhinolophina*. No mention was made of the genus *Aello*.

Using Gray's tribes, in more or less the same context, Bonaparte (1831:15) arranged *Mormops* (invalid emendation of *Mormoops* Leach by Cuvier, 1829) with the *Phyllostomina* and *Aello* with the *Noctilionina*. It is interesting to note that Bonaparte placed all bats known to him in the family Vespertiliones.

Gray (1838), in a revision of the genera of bats (Vespertilionidae), followed Bonaparte's arrangement of *Aello* and *Mormoops* and incorporated Spix's (1823) terms Anistiophori (nose appendage absent) and Istiophori (nose appendage present) as subheadings within the family. Also, in this paper, Gray described a new mormoopid genus and species, *Pteronotus Davyi*, which he placed after *Aello* in the tribe Noctilionina (Anistiophori).

Gray (1839) reported on a small collection of mammals made by W. S. MacLeay in Cuba and described an additional mormoopid genus, *Chilonycteris*, based on the species *C. Macleayii*. Also present in this small collection was the second known example of *Mormoops* Leach. Until that time, taxonomists had been misled by Leach's characterization of *Mormoops* as having "a single nose-leaf confluent with the ears." For this reason, *Mormoops* was consistently referred to the family Phyllostomatidae (or some similar grouping). With the additional specimen in hand, Gray (1839:3) concluded that *Mormoops* did not have a nose-leaf, and that it was closely allied to the Noctilionina. In revising his arrangement of 1838, Gray (1839:3) wrote: "This [*Mormoops*] and the new Cuban genus *Chilonycteris*, which agrees with it in many particulars, will together form a new section in this group [Noctilionina] characterized by the expansion of the lower lip and the convex and rounded form of the skull." This appears to be the first time that *Chilonycteris* and *Mormoops* were associated in a distinct group, but no reference was made to *Aello* or *Pteronotus*.

Meanwhile, Wagner (1839) proposed a classification in which he associated dermopterans (suborder Dermoptera) with bats (suborder Chiroptera) in the order Volitantia. Bats were divided into three families (Frugivora, Istiophora, and Gymnorhina). The latter two families were further partitioned into tribes for which Wagner used the term "Sippen." The tribes Desmodina and Phyllostomata were contained within the Istiophora. The Gymnorhina was divided into three tribes (Brachyura, Gymnura, and Vespertilionina) based primarily on the nature of the tail. The genera *Mormops [sic]*, *Chilonycteris*, and *Noctilio* (pp. 445-449), were assigned to the Brachyura.

An arrangement presented by Lesson (1842:12-36), illustrates the extreme differences of opinion among taxonomists of that period. Five families of bats,

presumably those of Gray (1838) or Bonaparte (1831), were assigned to the tribe Chiroptera, which along with the Bimana and Quadrumana comprised the order Mastomonodelphie in the subclass Mammiferes Normanx. The only mormoopid genera treated were *Aello* and *Mormoops*, arranged in the Noctilioneae and Phyllostomineae, respectively.

No major changes were made in Gray's classification between 1840 and 1860. In this period, however, many new species were described, particularly from the Americas. Relevant to this discussion are the descriptions of the following: the genus *Lobostoma* and the species *L. cinnamomeum* and *L. quadridens* by Gundlach (1840:356-358); three new species of *Chilonycteris (gymnonotus, personata,* and *rubiginosa)* from the Mato Grosso region of Brasil by Wagner (1843:367); *Chilonycteris fuliginosa* from Haiti by Gray (1843a: 20), which according to the describer resembled *C. macleayi*; and a new genus and species *Phyllodia parnellii* from Jamaica, which Gray (1843b:50) allied with *Mormoops* and *Chilonycteris.*

Peters (1856) re-evaluated Leach's description of *Mormoops blainvillii,* concluded that Leach was correct concerning the presence of a nose-leaf, and placed *Mormoops* in the family *Phyllostomata.* Later, Peters (1864:381-382) described *Mormoops megalophylla* from México and referred *Lobostoma cinnamomeum* Gundlach to synonymy under *Mormops blainvillii* Peters, 1856 (not Leach, 1821). Redescription of taxa was a common practice in this period, and *M. blainvillii* Peters appears frequently in the literature of the last half of the Nineteenth Century (primarily in papers by Peters). Although Peters gave a lengthy characterization of *blainvillii,* he clearly stated (1856:411) this his material was no different from the bat described originally by Leach in 1821.

M. H. de Saussure (1860:286-293) allocated the genera *Mormops* and *Chilonycteris* to "Sous-tribu" *Mormopsins* in the "Tribu" Noctilioniens of the family Vespertilionides. This arrangement appears to be the first in which the mormoopids were allied within a distinct family-group. Also within the framework of this same tribe, Saussure erected two other subtribes, *Noctilionins* and *Emballonurins.* The phyllostomatids were treated together as the only other apparent "family" in his classification.

Koch (1862-63) envisioned the Mammalia as comprising four major groups or "Reiche." One of these, the Primates, he divided into four orders ("Ordnungen")—Bimana, Quadrumana, Hemipitheci (including Dermoptera), and Chiroptera. In a section concerning families and genera of Chiroptera, he (p. 298) erected two suborders—Carpophagen and Entomophagen; the latter containing the families Gymnorrhina and Istiophora. In the Brachyura, a subdivision of the family Gymnorrhina, Koch (pp. 303-304) placed *Mormops, Chilonycteris, Phyllodia, Aello,* and *Pteronotus* along with several other genera not currently associated with mormoopids. Nowhere in his classification did Koch (1861) use the term "Mormopida" which does appear later (p. 358) in a section concerned with types of European bats and has been quoted as the first family-group name for the mormoopids. The relevance of this name will be discussed at the end of this review.

At this point in the history of chiropteran classification, both Peters and Gray recognized the distinctness of mormoopid bats. Peters (1865:257) placed *Mormops* Leach, *Chilonycteris* Gray (including *Lobostoma* Gundlach), and *Pteronotus* Gray into a subfamily group, which he termed *Mormopes,* in the family Phyllostomata. In a synopsis of the vespertilionid and noctilionid genera, his last major contribution to chiropteran classification, Gray (1866a) placed *Mormops* in a tribe termed *Mor-*

mopsina. The genera *Phyllodia, Chilonycteris*, and *Pteronotus* were allocated to another, related tribe, *Phyllodiana*; both tribes appear in the family Noctilionidae.

In all of the classifications up to this time, *Aello* Leach was overlooked or mentioned only in passing, probably due to a misplaced holotype. Gray (1866b) located and re-examined this crucial specimen. Although he did not go so far as to synonymize *Aello* with *Mormoops*, Gray did note that *Aello cuvieri* agreed with *Lobostoma cinnamomeum* Gundlach, which he supposed was only a variety of *Chilonycteris macleayii*. Peters (1866) also re-examined the holotype of *Aello cuvieri* and found it to agree completely with *Mormoops blainvillii*. He disregarded this fact on the assumption that some mix-up had occurred and the specimen labeled as the holotype of *Aello cuvieri* was not in fact the holotype of that taxon.

Fitzinger (1870) assigned mormoopid bats, except *Pteronotus*, to the group Noctiliones in the family Vespertilionidae. For some reason he placed *Pteronotus* in the group Molossi of this same family. Gill (1872), in his arrangement of the mammalian families, listed the family-group name Mormopidae, but gave no indication of included genera.

A milestone in bat classification was Dobson's (1875) conspectus, which was the first attempt to interpret phylogenetic relationships within the Chiroptera. Employing various anatomical characters, Dobson (1875:345-346) divided the order into two suborders, Megachiroptera and Microchiroptera. He postulated two distinct lines of descent ("alliances") within the suborder Microchiroptera; the Vespertilionidae and Emballonuridae were placed near the bases of these two lines. Only the emballonurine line, containing the families Emballonuridae and Phyllostomatidae, is of importance to this discussion; the family Noctilionidae was eliminated, and the genus *Noctilio* was placed in the family Emballonuridae. Dobson divided the Phyllostomidae into two subfamilies (Lobostominae and Phyllostominae), each of which was subdivided into groups of allied genera. The genera *Mormoops, Chilonycteris*, and *Pteronotus* were arranged in the group Mormopes of the subfamily Lobostominae. The remaining subfamily was divided into four groups of genera—Vampyri, Glossophagae, Stenodermata, Desmodontes. As regards the relationships within the emballonurine line, Dobson thought the Emballonuridae and Phyllostomidae were linked through the Noctiliones *(Noctilio)* and Mormopes *(Chilonycteris)*. With few modifications, this classification was the same used by Dobson (1878), in which only two genera, *Chilonycteris* (including *Pteronotus*) and *Mormoops* (including *Aello*), were recognized in the subfamily Lobostominae (group Mormopes).

Near the turn of the century, important classifications were proposed by Flower and Lydekker (1891), Winge (1892), and Trouessart (1897). The arrangement presented by Flower and Lydekker is only slightly different from Dobson's (1875, 1878), but is of nomenclatural importance because it is the first apparent usage of the subfamilial name Chilonycterinae for the genera *Chilonycteris* and *Mormoops*. Winge's (1892) treatment of the Chiroptera is notable because he removed the genus *Noctilio* from the family Emballonuridae and associated it with the mormoopids in his second "main division" of the family Phyllostomatidae that he termed *Mormopini*. He felt that the *Mormopini* were somewhat more specialized than bats of his other division *(Phyllostomatini)*. Trouessart (1897) placed the genera *Chilonycteris, Pteronotus*, and *Mormoops* in a subfamily (Mormopinae) of the family Emballonuridae. The genus *Noctilio* was assigned to one of the sections (Noctilioneae) of the subfamily Emballonurinae.

Mormoopid genera were reviewed taxonomically by Rehn (1902, 1904a, 1904b). Rehn (1902) studied 49 specimens of *Mormoops* and asserted that *Mormoops, Chilonycteris,* and *Dermonotus* (proposed as a replacement name by Gill, 1901, for the supposedly preoccupied *Pteronotus*) comprised a well-defined subfamily within the *Phyllostomatidae.* To this subfamily, he (p. 162) applied the name Mormoopinae (see also Rehn, 1901). He rejected Lobostominae Dobson, 1875, on the grounds that *Lobostoma* Gundlach, 1840, "is a synonym of *Mormoops* and *Chilonycteris.*" Under the current code of nomenclature, the name Lobostominae is rejected for other reasons as explained below. Rehn (1904a) reviewed *Chilonycteris,* based on an examination of 103 specimens, and (1904b) *Dermonotus* (= *Pteronotus*), based on 36 individuals.

The taxonomic arrangement of Miller (1907) is the basis for the current classification of the order as presented by Simpson (1945), Hall and Kelson (1959), and Koopman and Cockrum (1967). Miller's classification was by no means novel in its conception, having been drawn in part from the earlier works of Gray, Dobson, Winge, and others. The order Chiroptera was arranged into two suborders (as defined by Dobson, 1875), 17 families, and 19 subfamilies based on the comparative anatomy of the wing, shoulder girdle, sternum and associated ribs, and the number and structure of the teeth. In this classification, Miller placed the genera *Chilonycteris, Pteronotus,* and *Mormoops* in the subfamily Chilonycterinae (Flower and Lydekker, 1891) of the family Phyllostomidae, which he further divided into six other subfamilies—Phyllostominae, Glossophaginae, Hemiderminae (= Carolliinae), Sturnirinae, Stenoderminae, and Phyllonycterinae. Simpson (1945) retained Miller's classification, modifying it by grouping the families into superfamilial categories based on the "families" of Winge (1892).

Recently, Dalquest and Werner (1954) accorded full familial rank to the mormoopid genera and used the name Chilonycteridae. Their conclusions (to be considered in somewhat greater detail below) were based on the histological aspects of facial glands of North American bats. This study seems to have been overlooked by many mammalian systematists.

According to The International Code of Zoological Nomenclature, 1958, Article 29(d): "A family-group taxon formed by the union of two or more taxa of that group takes the oldest valid family-group name among those of its components, with change of termination if required." From the foregoing historical review, it is clear that *Mormoops* was used consistently during the last half of the Nineteenth and early part of the Twentieth centuries as the basis for various family-group names, but the name Chilonycterinae was first used by Flower and Lydekker (1891). In fact, family-group names based on the genera *Phyllodia* (Phyllodiana Gray, 1866a) and *Lobostoma* (Lobostominae Dobson, 1875) predate Chilonycterinae. Therefore, the family-group name for the bats here treated should be based on the generic name *Mormoops* Leach, by priority, rather than on *Phyllodia, Chilonycteris,* or *Lobostoma.*

The selection of authorship for the earliest family-group based on *Mormoops* requires further consideration. Palmer (1904:754) listed Mormopida Koch (1862-63) as the first apparent usage of *Mormoops* as the basis of a family-group name. Both Miller (1907: 118) and Simpson (1945:57) also cited this usage in their familial synonymies. Miller (1907) took his citation directly from Palmer (1904) and Simpson (1945) seems to have done the same. The name Mormopida of Koch appears once on page 358 in the following context: "*Eine davon* (Synotus barbastel-

lus) *wird zwar von anderen Forschern wegen der durch die stellung der Nasenlocher bedingten Physiognomie zu den Trutzern (Mormopida) gestellt; da wir aber das Verhaltnisz des Schwanzes zur Periscelis bei der Eintheilung der Gruppen festhalten mussen, so kann die Gattung Synotus nur bei den Vespertilionen untergebracht werden.*" This is the only mention of the term "Mormopida" in Koch's entire paper nor does it appear in his taxonomic arrangement, discussed above. Inasmuch as this usage was vague and without indication of included kinds, the name "Mormopida" of Koch must be designated a *nomen dubium.*

As noted previously, Saussure (1860: 286), clearly allocated the genera *Mormoops* and *Chilonycteris* to a family-group (Sous-tribu) Mormopsins. Saussure (1860) seems to be the first authority to so group these bats and, therefore, must be recognized as the author of the family-group name. In accordance with Article 10(c) of the Code, the name Mormopsins must be fully latinized to Mormoopidae—*Mormo* (ghost), ops (face) = *Mormoops,* nominative singular; *Mormoop/os,* genitive suffix plus -idae = Mormoopidae). This familial name is firmly based on priority. Furthermore, Rehn (1902, 1904a, and 1904b), the most recent and major reviser of the entire group, used the name Mormoopinae. Finally, use of this name in preference to Chilonycteridae is in the interest of nomenclatural stability.

As earlier noted, I have raised the group to full familial status. My reasons for doing so are presented in the following section. Henceforth, I shall refer to these bats as the Mormoopidae or mormoopid bats, but may, from time to time, use the terms "chilonycterine" or "Chilonycterinae" in directly quoted passages.

ANALYSIS OF CHARACTERS

The genera *Chilonycteris* (including *Phyllodia*), *Pteronotus,* and *Mormoops* were placed together in the subfamily Chilonycterinae of the family Phyllostomidae by Miller (1907), who based his classification on a detailed study of the skeleton, particularly the wing, shoulder girdle, and structure of the tooth cusps. Although each family was characterized in detail, many characters mentioned were shared by several families. For example, by my count, the greater tuberosity or trochiter was described as large in size and articulating, in some fashion, with the scapula in 11 different families, seven of which occur in the New World. This "secondary articulation" is absent in the Mormoopidae. The distal end of the humerus was described for phyllostomatids in rather general terms (pp. 116-117): "epitrochlea moderately developed, usually with spinous process, capitulum distinctly out of line with the shaft." More or less the same wording was used to characterize the distal end of the humerus of at least six other New World families. Likewise, the presence of three bony phalanges in the third manal digit in phyllostomatids is shared with three other New World families.

Reduced to the essential common denominator, phyllostomatids can be characterized as those New World bats that possess a cutaneous nasal appendage, commonly referred to as the nose-leaf. Although generally well-developed, the nose-leaf may be greatly reduced as in the subfamilies Phyllonycterinae (including *Brachyphylla* as suggested by Taboada and Pine, 1969) and Desmodontinae (included in this family following the suggestion of Machado-Allison, 1967; and Forman *et al.*, 1968) and the stenodermine genus *Sphaeronycteris.* In another stenodermine genus *Centurio,* the nose-leaf is curiously contorted and nearly obscured by the many

intricate ridges and folds. The tiny wart-like bumps above and between the nostrils of mormoopids (Fig. 10) have been interpreted as a rudimentary nose-leaf (notably by Leach and Peters). Phyllostomatids also are unique among New World Chiroptera in their adaptive radiation. From the outset of this study, it was apparent that the only possible reason to consider mormoopids as members of the family Phyllostomatidae was to assume the presence of a rudimentary nose-leaf.

One of my major objectives has been to test the arrangement of the mormoopid genera as a family distinct from the Phyllostomatidae. In doing so, I tried to avoid use of classical characters employed by Miller (1907) and others and sought new characteristics on which a classification could be constructed. Like my predecessors, I turned to the skeleton and soft anatomy in search of such characters. In order to understand the latitude of variation of a particular character, I examined representatives, both generalized and specialized, of every New World family and several selected Old World groups. Unfortunately, there is a paucity of complete skeletal material in the mammalian collections of major North American institutions, and the examination of more than one representative of a taxon was not always possible. In arranging mormoopids as a distinct family, I relied heavily on the following characters: 1) structure of the distal end of the humerus; 2) structure of the proximal end of the humerus and its relationship with the scapula; 3) structure of the proximal end of the femur; and 4) structure and shape of the tragus. When possible, I have indicated the functional significance of the characteristics employed in this study. However, our knowledge of bats is still relatively limited and the functional significance of characters studied was not always apparent. A further handicap is the virtual absence of a fossil record; the evolutionary stage of a given character only could be surmised.

In the transition from a terrestrial mode of life to a volant habit, many aspects of the chiropteran anatomy have undergone marked adaptive changes. The most noticeable of these modifications are changes in the forelimbs and pectoral girdle. As might be expected, these changes involve more than elongation of the forearm and phalangeal elements to form a wing. Whereas the forelimb of quadrupedal, terrestrial mammals functions in the support of the body as well as in locomotion, the principal function of the forelimb in bats is the latter. In addition, the operational plane of the forelimbs is vertical to the longitudinal axis in terrestrial mammals, but in bats this plane has been changed to a lateral position, due to a 90-degree dorsal rotation of the forelimb. Muscles that formerly functioned to suspend the body between the forelimbs have been modified to increase the efficiency of the wing beat. The three major points of articulation in the wing (scapula-humerus, humerus-radius, and radius-carpus) also have undergone marked changes. Processes on the wing bones that normally are lateral or medial to the body in terrestrial mammals become dorsal and ventral, respectively, in bats.

Distal End of Humerus

The structure of the distal end of the humerus provides several interesting features that seem to be of taxonomic value. Miller (1907:13-17) discussed the modifications of the humerus with reference to its structure in the Megachiroptera and Microchiroptera. He was primarily concerned with the size of the trochiter and trochin (see Fig. 6 for definition of terms) and their position relative to the head of the humerus. Distally, he noted the size and position of the capitulum, the development of the external (lateral epicondyle) and internal condyles (medial epicondyle),

and the presence or absence of a spinous process. Lawrence (1943) noted the value of the humerus as a generic character in several vespertilionids. Some paleontologists, Revilliod (1917a, 1917b, 1920, and 1922) and Savage (1951), have used the humerus as an indicator of familial alliances.

Before considering the distal end of the humerus in detail, it is useful to consider the elbow joint of bats and the general modifications that have taken place. The humerus and radius are the two major elements that form this joint. In bats the ulna, which forms the largest part of the forearm segment in terrestrial mammals, is greatly reduced in size and is represented by little more than the olecranon process. This process, important in bats as well as in terrestrial mammals, is the point of insertion for the tendons of the *M. triceps brachii,* a major extensor of the forearm.

The most conspicuous part of the distal end of the humerus is the spool-shaped articular surface. In terrestrial mammals this surface can be divided into two parts—the capitulum, which normally articulates with the proximal portion of the radius, and the trochlea, which forms the articular surface for the ulna. Inasmuch as the ulna is virtually absent in bats, the radius has expanded medially (that is, ventrally) to articulate with the trochlea in addition to the capitulum (Fig. 5). The ulna, although reduced, still maintains a small articular surface that fits into a depression on the postero-medial edge of the triangular articular surface of the radius and is confluent with that surface (Fig. 5, E-H).

The result of these modifications has been to strengthen the elbow joint. The motions of pronation and supination, advantageous to some mammals, are completely lost by the Chiroptera and the hingelike elbow joint is restricted to extension and flexion. Similar modifications that have produced the same sorts of results can be seen in the forelimbs of some ungulates, as noted by Gregory (1949).

In his diagnoses of each family, Miller (1907) used the term "spinous process." According to these diagnoses, every New World family had a spinous process of one sort or another. Considerable variation in structure is exhibited by New World genera with respect to the region medial to the distal articular facet, and for this reason I have found it useful to redefine the spinous process. First, in a number of bats there is a process that extends medially (ventrally) from the medial epicondyle and that could be called the ventral process, but to preserve conventional anatomical nomenclature I will refer to it as the medial process (Fig. 3). The length of this process may be equal to the width of the distal articular surface when well developed or may be short and compressed against the medial epicondyle when only weakly developed. In some bats there is an additional structure that extends distally from the tip of the medial process. Hereafter, I will refer to this structure as the distal spinous process (Fig. 3).

Capitulum and trochlea.—As mentioned above, Miller (1907) commented on the position of the capitulum and trochlea relative to the longitudinal axis of the humerus. In figures 3 and 4 it is evident that these articular surfaces may be displaced laterally (that is, dorsally) from the longitudinal axis or may be more or less bisected by this axis. On this basis alone, the Vespertilionidae (Fig. 3, R-S), Molossidae (Fig. 3, T-U), and the Emballonuridae (Fig. 3, A-C) may be separated from all other New World families (but the emballonurids do not resemble either the vespertilionids or molossids in other characters of the distal end of the humerus). The remaining families have an offset capitulum and trochlea, although in the genus *Noctilio* (Fig. 3D) and the mormoopid genera (Fig. 4) the capitulum and trochlea lie in a somewhat inter-

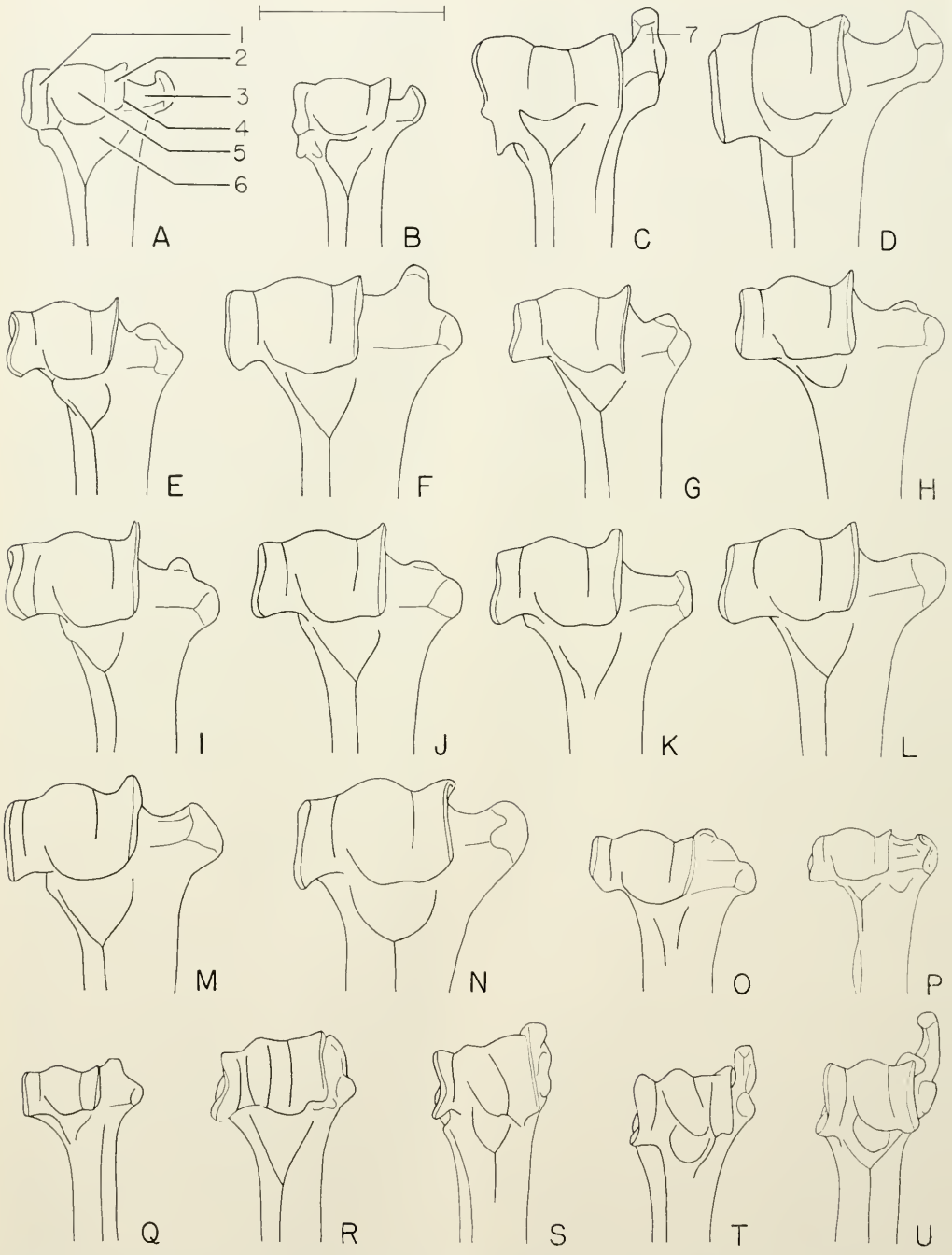


FIGURE 3. Anterior view of the distal end of the left humerus of representative New World bats as follows: A, *Rhynchonycteris naso;* B, *Balantiopteryx plicata;* C, *Diclidurus virgo;* D, *Noctilio labialis;* E, *Micronycteris sylvestris;* F, *Lonchorhina aurita;* G, *Glossophaga soricina;* H, *Anoura geoffroyi;* I, *Lonchophylla robusta;* J, *Carollia perspicillata;* K, *Sturnira lilium;* L, *Artibeus toltecus;* M, *Centurio senex;* N, *Desmodus rotundus;* O, *Natalus stramineus;* P, *Thyroptera tricolor;* Q, *Furipterus horrens;* R, *Myotis grisescens;* S, *Lasiurus borealis;* T, *Tadarida brasiliensis;* U, *Molossus molossus.* The labels on A and C refer to the following structures mentioned in text: 1, lateral surface of capitu-

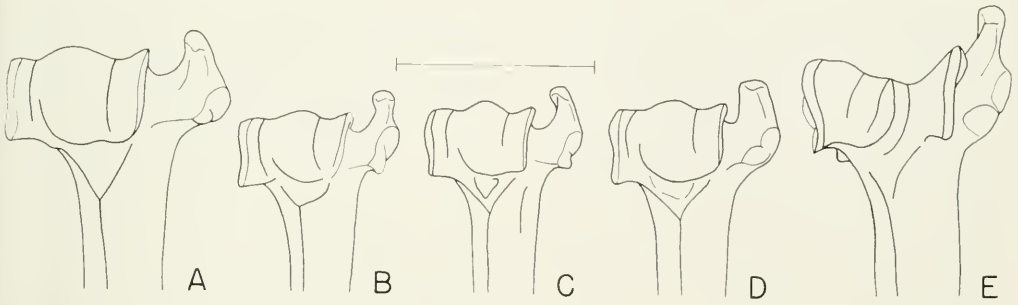


FIGURE 4. Anterior view of the distal end of the left humerus of five mormoopids: A, *Pteronotus parnellii;* B, *P. personatus;* C, *P. davyi;* D, *P. suapurensis;* E, *Moormoops megalophylla.* See text for discussion. The line above C is 4 mm in length.

mediate position. The lateral displacement of these distal articular facets seems to be correlated with the large size of the muscle mass of the forearm that originates from the medial process.

As I have mentioned, the distal articular surface is spool-shaped and in conjunction with the expanded proximal surface of the radius effectively restricts the elbow to a hinge-joint. During flight however, a great deal of air pressure must be sustained by this joint. Therefore, lateral (dorso-ventral) movement at this point must be minimized if the wing is to remain rigid and not buckle under these pressures.

The distal articular surfaces are variously shaped (Fig. 3). Miller (1907) also noted these differences, but failed to note their functional importance. It has already been stated that bats with heavy forearm muscle masses usually have rather well-developed medial processes. In these bats (phyllostomatids and emballonurids, for example) the distal articular surfaces are not markedly modified. The central part of the spool, the central portion of the capitulum, is spherical in phyllostomatids or slightly oblong in some emballonurids; the notable exception here is *Diclidurus* (Fig. 3C). The lateral part of the capitulum and the medial trochlea may be nearly equal in distal extension or the trochlea may extend somewhat farther distally than either part of the capitulum. At first glance, it would seem that this type of elbow joint (Fig. 5C) might be vulnerable to the excessive pressures that develop in this region during flight. However, in these bats the proximal forearm muscle mass may act as a binding and prohibit any appreciable lateral movement at this joint.

With the development of faster, more efficient modes of flight, the size of the forearm muscle mass is reduced and its functions replaced by automatic devices (discussed beyond). When this muscle mass is reduced, the elbow joint must be reinforced to withstand aerodynamic pressures. Accordingly, the articular surfaces of the elbow region have undergone several types of structural reorganization. The simplest of these is seen in *Pteronotus* (Fig. 4, A-D). The central part of the capitulum is slightly larger and the corresponding articular surface of the radius is deepened to form a "tongue-and-groove" arrangement. A reverse of this construction is seen in *Mormoops* (Fig. 4E) and *Diclidurus* (Fig. 3C). The

lum; 2, trochlea; 3, medial process; 4, medial epicondyle; 5, central surface of capitulum; 6, radial fossa; 7, distal spinous process. See text for discussion of distal end of the humerus. The line above B is 4 mm in length.

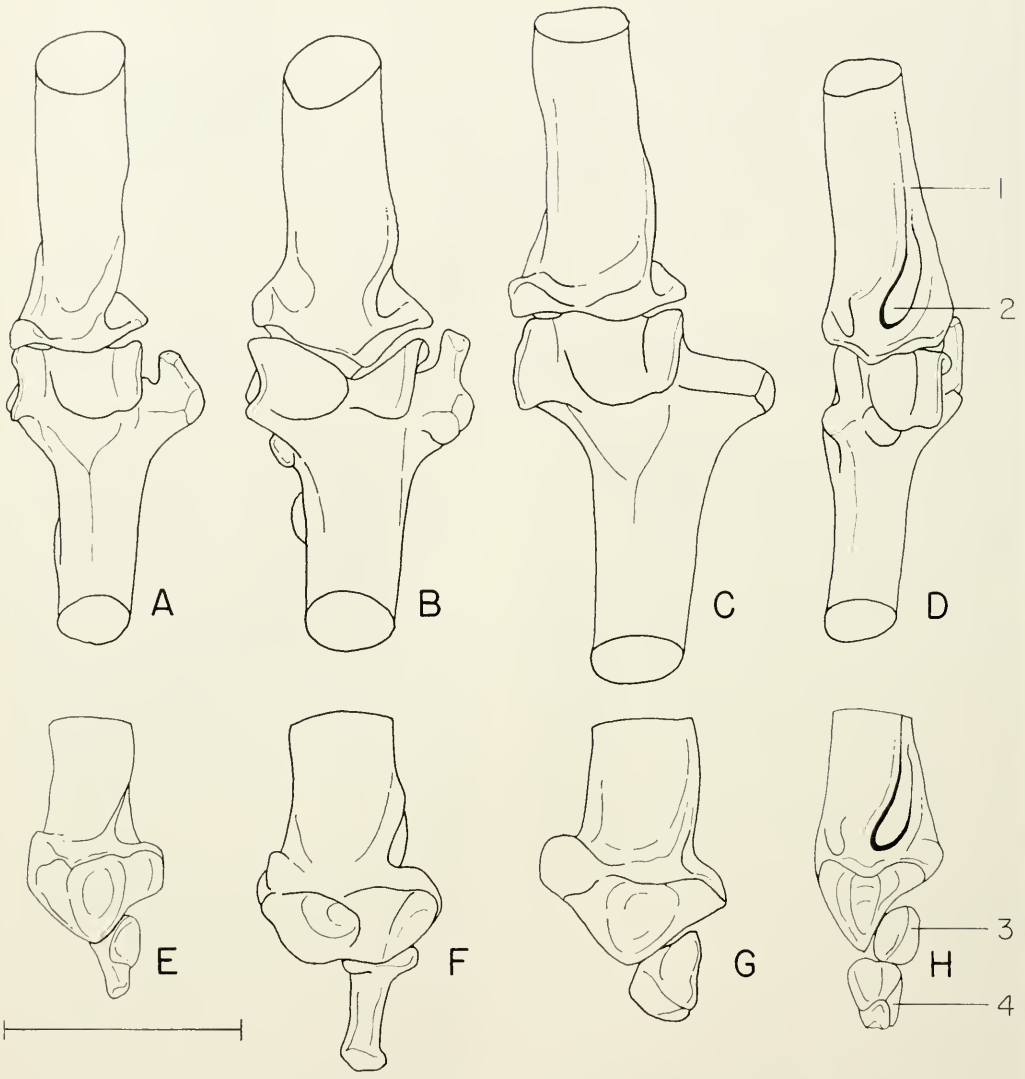


FIGURE 5. Anterior view of elbow region of four bats: A, *Pteronotus parnellii;* B, *Mormoops megalophylla;* C, *Artibeus toltecus;* D, *Molossus molossus.* Below each of these (E-H) the radius is figured to show the articular facets. The labels on D and H identify: 1, radius; 2, flexor fossa, into which the tendons of the *M. biceps brachii* and *M. brachialis* insert; 3, reduced ulna; 4, sesamoid bone. See text for discussion. The line below E is 4 mm in length.

central portion of the capitulum is reduced in size and the lateral part of the capitulum and the trochlea remain more or less unchanged. The portion of the radius that embraces the central capitulum is modified to fit into the scooped-out distal articular surface. Another modification of the "tongue-and-groove" arrangement is seen in the vespertilionids and molossids (Fig. 3, R-U), in which the rounded surface of the central capitulum becomes angular or narrowed and tilted diagonally. In conjunction with these structural modifications of the distal articular surface of the humerus, the groove in the proximal articular surface of the radius is deepened and shaped to correspond with the

central capitulum. All of these modifications in the structure of the spool-shaped articular surface of the distal end of the humerus increase the stability of the elbow joint by restricting lateral movement.

Spinous and medial processes.—Although features of the distal end of the humerus are important in grouping various taxa, other striking features are the structures located medially (that is, ventrally) to the capitulum and trochlea. These are the medial and distal spinous processes. The presence of a strong medial process is characteristic of the Phyllostomatidae (Fig. 3, E-N) in that this process is large and bulky and associated with a heavy forearm muscle mass. The medial process of the emballonurids (Fig. 3, A-C) is rather short and broad, and the extreme portion is curled distally. For the most part, the Noctilionidae (Fig. 3D) resembles the emballonurids in this respect. Curiously, in the genus *Diclidurus,* this region of the distal end of the humerus is greatly modified; the medial process is shortened, slanted distally, and gives rise to a short distal spinous process. In contrast, the medial process of vespertilionids (Fig. 3, R-S) is markedly smaller and less pronounced; the forearm muscle mass is also noticeably lighter. The bats of the family Molossidae (Fig. 3, T-U) have an extremely short medial process, but the distal spinous process is typical.

The Phyllostomatidae can be divided into two distinct groups, based on the shape of the medial process. One of these, the *Micronycteris*-line, has a bilobed medial process. The other, the *Phyllostomus*-line, exhibits a rather simple medial process that lacks any sign of bilobation. The *Micronycteris*-line includes the phyllostomatine genera *Micronycteris, Macrotus* (not figured), and *Lonchorhina,* the Glossophaginae (Fig. 3, G-I), and the Carollinae (Fig. 3J). The genera *Lonchorhina, Macrotus,* and *Lonchophylla* of the *Micronycteris*-line have departed slightly from the basic bilobed medial process by enlargement of the distal lobe to varying degrees. This lobe is particularly well-developed in *Lonchorhina* and superficially resembles the distal spinous process of mormoopid genera (Fig. 4). I was concerned, at first, by this distally projecting lobe and wondered if it might be an intermediate step toward the development of the distal spinous process as exemplified in the Mormoopidae. Terry A. Vaughan kindly consented to dissect several individuals of *Lonchorhina* with special reference to this question. After doing so he wrote (personal communication): ". . . the spinous process in the species *Lonchorhina aurita* is not homologous to that in the chilonycterines, at least if the muscle attachments are used as an indication of homology." In addition, this elongated lobe in the phyllostomatids does not appear to be associated with any automatic devices as discussed beyond.

Although skeletal material of the phyllostomatine genera *Tonatia, Mimom, Chrotopterus,* and *Vampyrum* was not available for examination, they are here grouped into the *Phyllostomus*-line along with *Phyllostomus, Trachops,* and *Phylloderma.* Other members of this group include the Sturnirinae, Stenoderminae, Phyllonycterinae, and probably the Desmodontinae.

Three small families, Natalidae, Furipteridae, and Thyropteridae, resemble the more generalized phyllostomatids in that the distal articular surface is offset from the shaft of the humerus and the medial process is moderately developed. This process is most strongly developed with respect to these three families in the genus *Thyroptera* (Fig. 3P), in which there are two small pits for muscle attachment in the extreme tip of the process. In both the genera *Natalus* and *Furipterus* (Fig. 3, O and Q, respectively), the medial process is noticeably different in comparison with

Thyroptera. It is moderately short with a prominent "spinous process" compressed against the medial epicondyle in the genus *Furipterus,* whereas in *Natalus* the medial process is wider and appears to be trilobed.

The Vespertilionidae and Molossidae have extremely short medial processes that are compressed against the medial epicondyle. Viewed from the medial side, the spool-shaped distal articulation has a deep fossa into which the medial process protrudes. Typically, vespertilionids do not exhibit distal spinous processes (see *Myotis,* Fig. 3R). However, in at least one genus, *Lasiurus* (Fig. 3S), there is a pronounced distal spinous process that is especially prominent in the large *Lasiurus cinereus;* the spinous process seems to be associated with sustained flight and is of interest inasmuch as these bats are well-known for their long migratory flights.

One of the most striking differences between the Vespertilionidae and Molossidae with regard to the distal end of the humerus is the presence of a long, well-developed distal spinous process in the latter family. Among the molossid genera examined in this study, *Tadarida* (Fig. 3T) exhibited the shortest distal spinous process and *Molossus molossus* (Fig. 3U) had the longest.

The medial process of the Mormoopidae is of moderate length in the species of the genus *Pteronotus* (Fig. 4, A-D) and markedly shortened in *Mormoops.* In all mormoopid genera, the distal spinous process is well developed and projects well beyond the medial epicondyle and distal articular surface. As regards the distal end of the humerus, the Mormoopidae is as distinct from the Phyllostomatidae as the latter is from any other family.

Functional significance of the distal end of the humerus.—The distal end of the humerus, in conjunction with the radius and to a certain extent the vestigial ulna, forms the articular joint on which the forearm pivots. In addition, muscles that control the movement of the manus originate from this region. During the downstroke (or power stroke), this region must be rigid in order to withstand the air pressures from below and obtain optimal lift from energy expended by the pectoral and associated muscles. During the upstroke, this region, along with the carpus, is flexed to allow for recovery of the wing in preparation for the subsequent power stroke.

In considering the functional significance of the distal end of the humerus, it is useful to review some of the mechanisms and also the evolution of chiropteran flight. Owing to the paucity of a fossil record for bats (the scanty fossil remains reveal little about the actual transition to a volant habit), the student of chiropteran functional anatomy must speculate on the evolution of flight based on observations of living representatives. The oldest known fossil (*Icaronycteris index* Jepsen, from the early Eocene of Wyoming) is clearly a full-fledged bat, as also are the two Old World Eocene fossils, *Archaeonycteris* Revilliod and *Palaeochiropteryx* Revilliod.

The early precursors of the Chiroptera probably were arboreal insectivores capable of short, gliding "fluttery" flights in pursuit of small flying insects. The bony structure of the forelimbs of these early ancestors may not have been noticeably different from those of other arboreal, non-gliding kinds; this is to say, the ulna may have been a moderately well-developed bone and the distal articular surfaces of the humerus still possessed both radial and ulnar facets. The medial process may have been triangular and supported a rather massive forearm muscle mass. A comparable situation in which morphological appearance does not necessarily reflect differences in behavior exists today between tree squirrels of the genus *Sciurus* and the gliding squirrels of the genus *Glaucomys.* The early precursors of

bats may have been nocturnal or, as seems more likely to me, crepuscular, becoming nocturnal as appropriate devices for acoustic orientation were developed.

The wing was formed by an elongation of the forearm and manal elements and, in the course of its formation, probably was "flapped" with varying degrees of success—from clumsy fluttering to sustained flight with a relatively stable wing beat. Flexing and extending of the wing in these early bats probably was accomplished through strict muscle control. As mentioned above, the forearm muscle mass was probably relatively heavy in the early bats and the medial process well developed to support this musculature. Revilliod (1917a:173, fig. 9) illustrated the distal end of the humerus of *Palaeochiropteryx spiegeli* in which the distal articular surface is almost completely set to one side of the longitudinal axis of the shaft and the medial process is massive and must have supported a heavy forearm musculature. Inasmuch as the medial process was evidently large in the early bats and is also large in those living groups that possess a generalized mode of flight, I believe that the presence of such a well-developed medial process is an indicator of primitiveness. I therefore regard the Phyllostomatidae as a generalized group of bats with respect to the distal end of the humerus.

As bats continued to adapt to the aerial niche, there evolved more efficient modes of flight. In some, efficiency improved through slight modifications of pre-existing structures. One of the more important was the development of the distal spinous process which, in conjunction with the *M. flexor carpi ulnaris*, became involved in the automatic control of the flexion of the distal parts of the wing. In a generalized bat such as *Macrotus* (Phyllostomatidae), this muscle is large and has a heavy, fleshy belly (Vaughan, 1959:91), and the distal segment of the wing is flexed solely by muscular effort. In *Macrotus* as well as in several other phyllostomatids (Vaughan, personal communication), the origin of the *M. flexor carpi ulnaris* is from the proximal end of the ulna, the medial tip of the medial process, or from a combination of both. As Vaughan (1959:91) stated, the origin of this muscle is not affected by movements of the radius.

In contrast, Vaughan (1959:91) noted that the elastic belly of the *M. flexor carpi ulnaris* was relatively small in *Eumops perotis* and *Myotis velifer*, and that in *E. perotis* the elasticity of the muscle is reduced by a thick fascial sheath that envelops the belly portion and extends from the large tendons of origin and insertion. In *M. velifer*, there is a tendonous core that passes down the center of the belly from origin to insertion. In both of these rather specialized bats, the *M. flexor carpi ulnaris* originates from the tip of the distal spinous process and inserts on the pisiform, which in turn is firmly attached to the fifth metacarpal. The reduced elasticity of this muscle to a cable-like strand of connective tissue, as well as its attachments, allow it to flex the fifth digit and thereby the entire manus when the forearm (radius) is flexed by the *M. biceps brachii*. The spinous process acts as a proximal extension of the radius away from the center of rotation in the elbow joint. As the radius is flexed, the tip of the distal spinous process and the origin of the *M. flexor carpi ulnaris* travel through a wide arc, thereby flexing the fifth digit with little muscular effort. Similar automatic devices for the extension of the manus are discussed by Vaughan (1959: 81).

Aside from the energy conserved by such automatic devices, the heavy muscles that ultimately control the distal portion of the wing are located proximally, nearer the center of gravity, and the potential weight of the wing is

reduced. In addition, because the control is automatic, a certain amount of precision may be introduced into the wing beat. All of these factors contribute to the increased overall efficiency of flight.

In the Mormoopidae, the development of the distal spinous process and the structure of the *M. flexor carpi ulnaris* and their involvement in an automatic flexing device seem to be directly comparable to those discussed above for vespertilionids and molossids. The functional morphology of the forelimb of mormoopids was discussed by Vaughan and Bateman (1970). Their conclusions agree with the above, and they concluded that mormoopids have a much more specialized forelimb than phyllostomatids.

In summary, the construction and function of the distal end of the humerus appears to set the mormoopids apart from the Phyllostomatidae and other groups of bats. These differences likely relate to a somewhat more specialized mode of flight in mormoopids as compared to the rather generalized flight of phyllostomatids.

Proximal End of Humerus

In classifying bats, Miller (1907) evidently was greatly influenced by the structure of the proximal end of the humerus. In fact, the size of the greater tuberosity (trochiter) relative to the lesser tuberosity (trochin), and whether or not the trochiter impinged on the scapula, were major characters used in his classification. Aside from the head of the humerus, the greater and lesser tuberosities are the most prominent features of the proximal end of that bone. As mentioned above, Miller noted that the greater tuberosity was frequently larger than the lesser, and in most cases projected above (proximal) the head (Fig. 6). However, in several groups of bats—emballonurids (Fig. 6A) for example—the greater tuberosity barely rises above the head; in other families—Molossidae (Fig. 6I) for example—the greater tuberosity is extremely long and projects well above the head of the humerus. In those bats with long greater tuberosities, Miller also noted a peculiar articulation between this tuberosity and the scapula, anterior and medial to the glenoid fossa. He called this articulation a "secondary" or "double" articulation. According to Miller (p. 13), this unique articulation allowed for a stronger joint, while at the same time limiting motion to a single plane. However, Vaughan (1959: 54) pointed out that such an articulation would limit the movement of the humerus, not to a vertical plane as Miller evidently thought, but to a horizontal (antero-posterior) plane that, in Vaughan's estimation, could not produce the wing beat.

Vaughan (1959:72) interpreted the elongated greater tuberosity and scapular contact as a "locking" device to stop the upstroke and increase the efficiency of the power stroke. As the humerus reaches the peak of the upstroke, the greater tuberosity strikes the scapula and thereby transfers the force of the stroke to that bone. The scapula tends to rock upwards, lifting the lateral border as it absorbs this transfer of force. The coordinated contraction of the posterior division of the *M. serratus anterior* effectively stops the upstroke and starts the power stroke in a whiplash fashion. The power stroke, thus started, is carried through by the powerful *M. pectoralis* and *M. subscapularis*.

One of the major differences pointed out by Miller (1907:116-117) between mormoopids and phyllostomatids was the absence of the secondary articulation in the former. The greater tuberosity of phyllostomatids exceeds (proximally) the rounded head of the humerus (Fig. 6, C-D). Both the *M. supraspinatus* (elevates, abducts, and rotates humerus) and *M. infraspinatus* (flexes, abducts, and rotates humerus) insert on the tip of this process. In

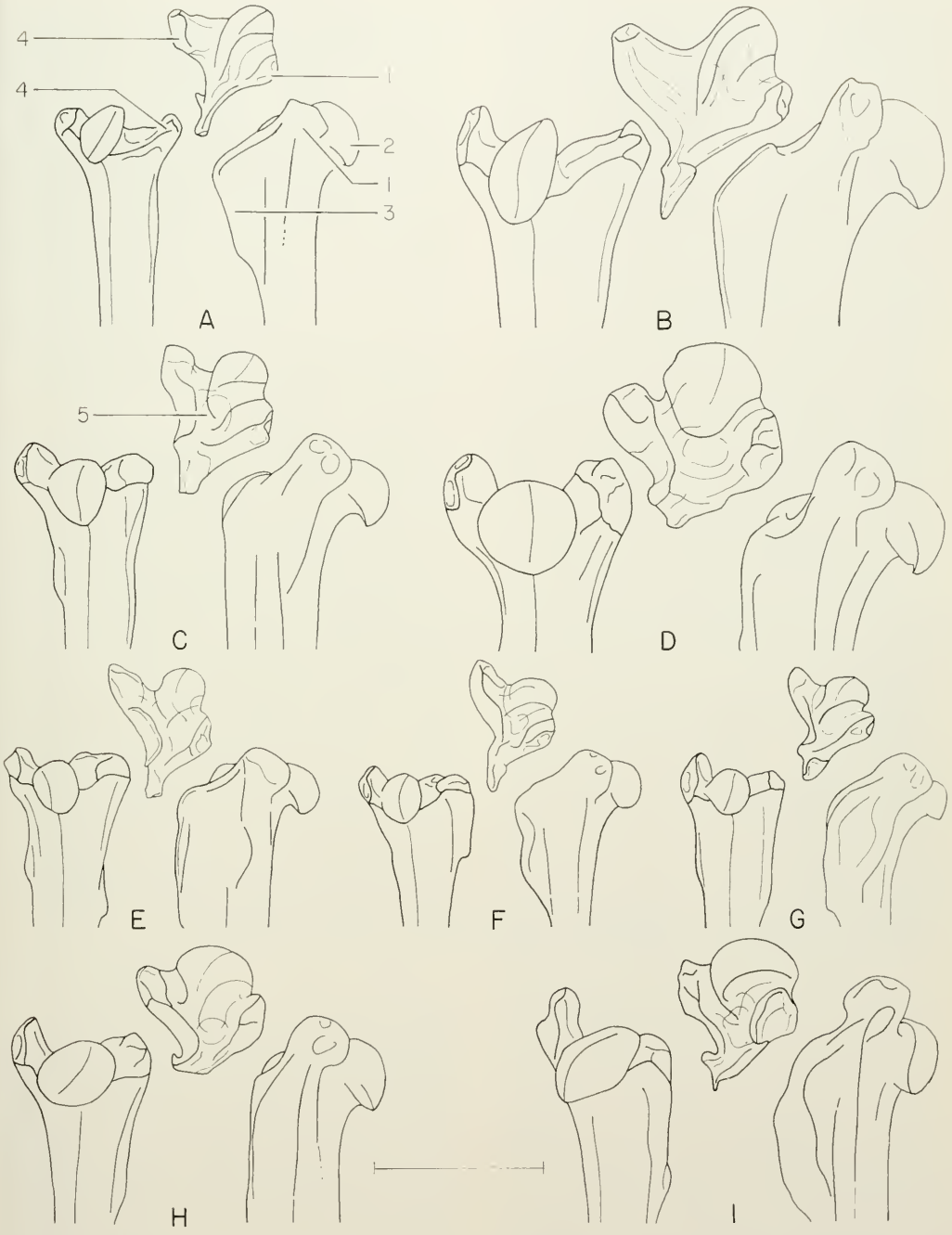


FIGURE 6. Medial, dorsal, and proximal (above) views of the proximal end of the humerus of representative New World bats: A, *Balantiopteryx plicata;* B, *Noctilio labialis;* C, *Micronycteris sylvestris;* D, *Desmodus rotundus;* E, *Natalus stramineus;* F, *Furipterus horrens;* G, *Thyroptera tricolor;* H, *Myotis grisescens;* I, *Molossus molossus.* The labels on A and C refer to the following structures mentioned in text: 1, greater tuberosity (trochiter); 2, head; 3, pectoral ridge; 4, lesser tuberosity (trochin); 5, supraglenoid fossa. See text for discussion of the proximal end of the humerus. The line between H and I is 4 mm in length.

accordance with the scheme described by Vaughan (1959:72) and outlined above, the greater tuberosity seems to make contact with the scapula during the terminal part of the upstroke. The locking function of this system is not so highly developed as in the vespertilionids or molossids and a greater degree of freedom is apparent. The rounded head of the humerus also may indicate a greater capability for rotation of the humerus in the phyllostomatids than in some of the more specialized families.

The lesser tuberosity of phyllostomatids projects ventrad and is connected to the shaft by a heavy ridge that eventually forms the medial ridge. The lesser tuberosity does not extend proximal to the head of the humerus in typical phyllostomatids, but in *Desmodus* (Fig. 6D) this process nearly equals the greater tuberosity in proximal extension. This modification may be related to the adducting quality of the *M. subscapularis* and the agility of this vampire in terrestrial locomotion. Other desmodontines, *Diphylla* and *Diaemus* (not figured), more closely resemble typical phyllostomatids in this respect. The two thick, bipinnate parts of the *M. subscapularis*, one of the powerful flight muscles, insert on the proximal surface of the lesser tuberosity. Other important muscles (*M. latissimus dorsi*, *M. teres major*, and parts of the *M. triceps*, for example) are associated with more distal portions of the medial ridge that forms the lesser tuberosity.

The head of the humerus in the Phyllostomatidae is continuous with the greater tuberosity (Fig. 6, C-D), and there is a well-defined depression (supraglenoid fossa) located anterior to the head and between the two tuberosities. The supraglenoid tuberosity of the scapula fits into this fossa (Vaughan, 1959:54), and contributes to the solid locking of the humerus and scapula at the terminus of the upstroke.

The Emballonuridae and Noctilionidae (Fig. 6, A and B, respectively) closely resemble each other in structure of the head of the humerus. In these two families the greater tuberosity barely extends beyond the head of the humerus and the lesser tuberosity, although widely separated from the head, remains even with or slightly distal to it. The head of the humerus is slightly canted and elliptical in shape (viewed medially). Viewed from the proximal end (Fig. 6, A-B), the head tapers anteriorly between the tuberosities and merges into the proximal root of the pectoral ridge. A supraglenoid fossa, as might be expected, is not present.

The structure of the proximal end of the humerus in the Natalidae, Furipteridae, and Thyropteridae (Fig. 6, E-G) more or less resembles that found in the Vespertilionidae. In all three families, the greater tuberosity exceeds the head of the humerus in proximal extension and the head is rather small and rounded. In the Vespertilionidae (Fig. 6H), the head of the humerus is large, round, and slightly tilted toward the lesser tuberosity, which is relatively short in its ventral extension. The supraglenoid fossa is present in all of these families. The medial ridge in *Furipterus* (Fig. 6F) is prominent, whereas this ridge gradually tapers into the shaft of the humerus in representatives of the other three.

The greatest modifications of the proximal end of the humerus are seen in the Molossidae (Fig. 6I). The greater tuberosity reaches its most extreme proximal extension in this group and the lesser tuberosity is reduced in size as in the Vespertilionidae. The head of the humerus is large and markedly tilted toward the lesser tuberosity. The supraglenoid fossa is deep and well defined by the proximal ridges of the greater and lesser tuberosities, which merge anterior to the head and form the proximal root of the pectoral ridge.

As noted by Miller (1907:119), the greater tuberosity of the mormoopid genera (Fig. 7) barely extends above

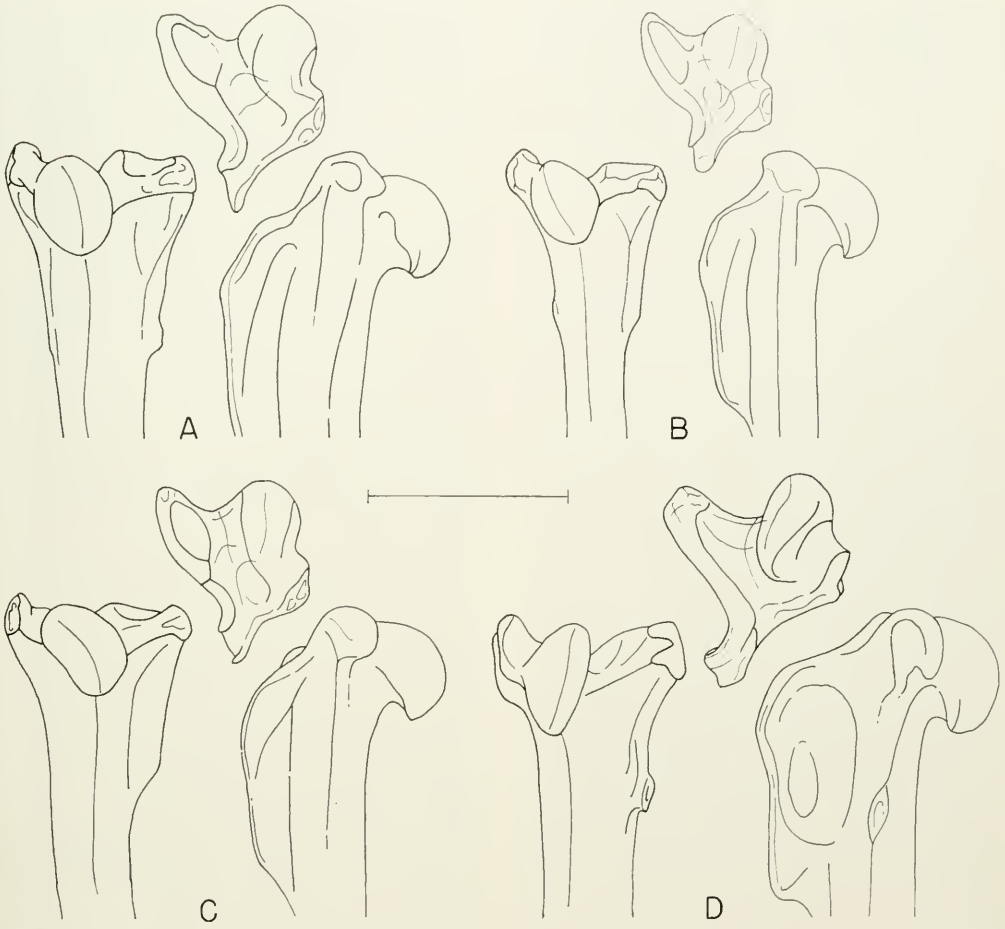


FIGURE 7. Medial, dorsal, and proximal (above) views of the proximal end of the humerus of four mormoopids: A, *Pteronotus parnellii;* B, *P. personatus;* C, *P. suapurensis;* D, *Mormoops megalophylla.* See text for discussion. The line in the middle of the figure is 4 mm in length.

the head of the humerus and no "secondary articulation" exists. In this respect, mormoopids resemble emballonurids and, to a certain extent, noctilionids. The lesser tuberosity is large and extends ventrad. In the species of *Pteronotus,* there is an elliptical pit that extends from the distal tip of the lesser tuberosity toward the proximal root of the pectoral ridge. The heavy anterior head of the *M. subscapularis* inserts into this pit. In the genus *Mormoops* (Fig. 7D), the lesser tuberosity extends slightly proximal and the pit for insertion of the *M. subscapularis* is not well defined. The head of the humerus is ovoid in *Pteronotus* (Fig. 7, A-C), and in *P. suapurensis* (Fig. 7C) the head is slightly inclined toward the greater tuberosity. The supraglenoid fossa is well developed in all mormoopid genera.

Adaptive significance of the proximal end of the humerus.—The proximal end of the humerus tends to be structurally more conservative than does the distal end in that a wide array of modifications is apparent distally (Figs. 3 and 4), but fewer, more subtle differences are seen at the proximal end (Figs. 6 and 7). The most extreme differentia-

tion is found in the Molossidae. The proximal part of the humerus is involved primarily in the up-and-down motion of the wing, whereas the distal segment is involved in manipulations of the distal elements of the wing. These different specific functions probably account for the differential development observed at each end of the humerus.

The proximal end of the humerus in the generalized terrestrial mammal has small tuberosities and the head is the most prominent structure. As mentioned above, the working plane of this humerus is horizontal, whereas that of the Chiroptera is vertical to the body. With the transition to a volant habit, the tuberosities migrated proximally to a position on either side of the head. In the Megachiroptera, the head of the humerus remains the single most prominent feature of the proximal end, but the tuberosities are present on either side. The greater degree of mobility allowed by the large, rounded head and small tuberosities is well illustrated by Kulzer (1968). In this paper, which deals with flight in *Eidolon helvum*, one individual is pictured at the peak of the upstroke. In this position, the elbow and wrist joints of each wing nearly touch over the back. To my knowledge, no microchiropteran, fossil or living, exhibits such a primitive stage in the structure of the humerus as seen in the Megachiroptera. Revilliod (1917a:172, fig. 8) illustrated a fragment of the right proximal end of the humerus of *Palaeochiropteryx tupaiodon* with the greater tuberosity intact. The head was apparently rounded and both tuberosities (lesser incompletely preserved) were prominent, although the greater barely extended above the head. The structure of this humerus resembles to some extent that found in living pteropodids and even phyllostomatids. However, judging from the structure of the humerus, *Palaeochiropteryx* probably was a more generalized bat than any living species.

Among living Microchiroptera the Emballonuridae, Noctilionidae, and Mormoopidae could be classed as primitive in that they lack a proximal extension of the greater tuberosity. The next stage in the specialization of the proximal portion of the humerus is probably best exemplified by the Phyllostomatidae, in which the greater tuberosity is extended proximally and probably contacts the scapula at some late phase in the wing beat. Next, and only slightly differentiated from this previous stage, would be the condition found in the Natalidae, Furipteridae, Thyropteridae, and Vespertilionidae. Finally, the ultimate stage of specialization of the proximal end of the humerus is seen in the Molossidae.

Miller (1907) failed to distinguish among the differences in the proximal end of the humerus; he simply referred to them as "secondary articulations" or "double articulations." Walton and Walton (1968:17-18) also studied the osteology of the wing elements in phyllostomatids and seem to regard Miller's use of the two terms "secondary" and "double" as an indication of two distinct articulations. Inasmuch as Miller made no distinction, I do not believe one was intended. I am convinced, after examining bony structures in many representatives of New World families, that there is more involved in the evolution of the shoulder joint than simply the elongation of the greater tuberosity and its relationship with the scapula. The shape of the head of the humerus and the depth of the supraglenoid fossa, for example, also must play an important role.

With respect to the proximal end of the humerus, mormoopids are more generalized than are phyllostomatids. Superficial dissections of *Pteronotus suapurensis* and *Artibeus lituratus* indicate only minor differences in the primary musculature of the shoulder region. As described above, there are some special provisions (oval pit in lesser tuberos-

ity) for the insertion of the *M. subscapularis* in the mormoopids (Fig. 7). The insertion of this muscle in *Artibeus lituratus* and *Macrotus waterhousii* (Vaughan, 1959:74) seems to correspond with that of the Mormoopidae.

The head of the humerus is round and centrally positioned in phyllostomatids, but it is oblong and somewhat tilted in the Mormoopidae, thereby indicating some degree of specialization in the latter. The supraglenoid fossa is present in the phyllostomatids, although relatively shallow. The modifications seen in mormoopids probably result in less freedom of rotation at the shoulder joint than in phyllostomatids. Freedom of movement in the latter may be related to a higher degree of maneuverability, because these bats normally fly in and around dense vegetation. As concerns the Mormoopidae, modifications of the distal end of the humerus result in increased precision in the wing beat and consequently a swifter mode of flight than found in phyllostomatids. By way of comparison, molossid bats illustrate the greatest degree of modification in the head of the humerus in that it is markedly oblique in shape, the supraglenoid fossa is deep, and the greater tuberosity is extremely elongate (Fig. 6I). It is my opinion that the long greater tuberosity, deep supraglenoid fossa, and oblique head of the humerus in the Molossidae restrict motion of the humerus to a slightly different plane than in other bats—a plane that seems to be somewhat more antero-posteriorly oriented than the normal up-and-down wing beat of the others.

In conclusion, Miller's term "secondary articulation" does not seem generally applicable to the humero-scapular relationships. Mormoopids lack any such "articulation" insofar as the greater tuberosity is concerned. Phyllostomatids and other groups with elongated greater tuberosities probably benefit from some sort of "weak" relationship with the scapula. The term "articulation" is poorly chosen in this context, and Vaughan (personal communication) prefers the term "locking device." More research on the chiropteran shoulder joint is indicated.

Proximal End of Femur

Vaughan (1959) considered the anatomy of the hind limbs of *Eumops, Myotis,* and *Macrotus* and showed that they play an important role in flight, while retaining much of their capability to function in terrestrial locomotion. As was the case with the forelimbs, the hind limbs of bats have been relieved of much of the weight-bearing responsibility characteristic of terrestrial mammals. The femur has rotated nearly 180 degrees dorsad and the whole limb has taken on a saurian posture, with the pes directed laterally and the knee joint dorso-laterally. The head of the femur in most terrestrial mammals projects mediad and the greater trochanter extends proximally beyond the knob-like articular process. The lesser trochanter occupies a position well below (distal) the level of either the head or the greater trochanter. In the Chiroptera, the head of the femur is the most prominent feature of the proximal end of this bone. It is rounded and directed slightly mediad, and apparently (due to this superior position) is capable of a great deal of rotation and freedom of movement.

The variation in structure of the proximal end of the femur, like that of the proximal end of the humerus, seems to be conservative. Major features of this portion of the femur are the size of the greater and lesser trochanters and the position of the head of the femur. With the exception of the mormoopids (Fig. 8, F-K), all bats examined in my study have two well-developed trochanters that are located on the lateral surface of the femur and are about equal in size. The head lies between the trochanters, along the longitudinal axis of

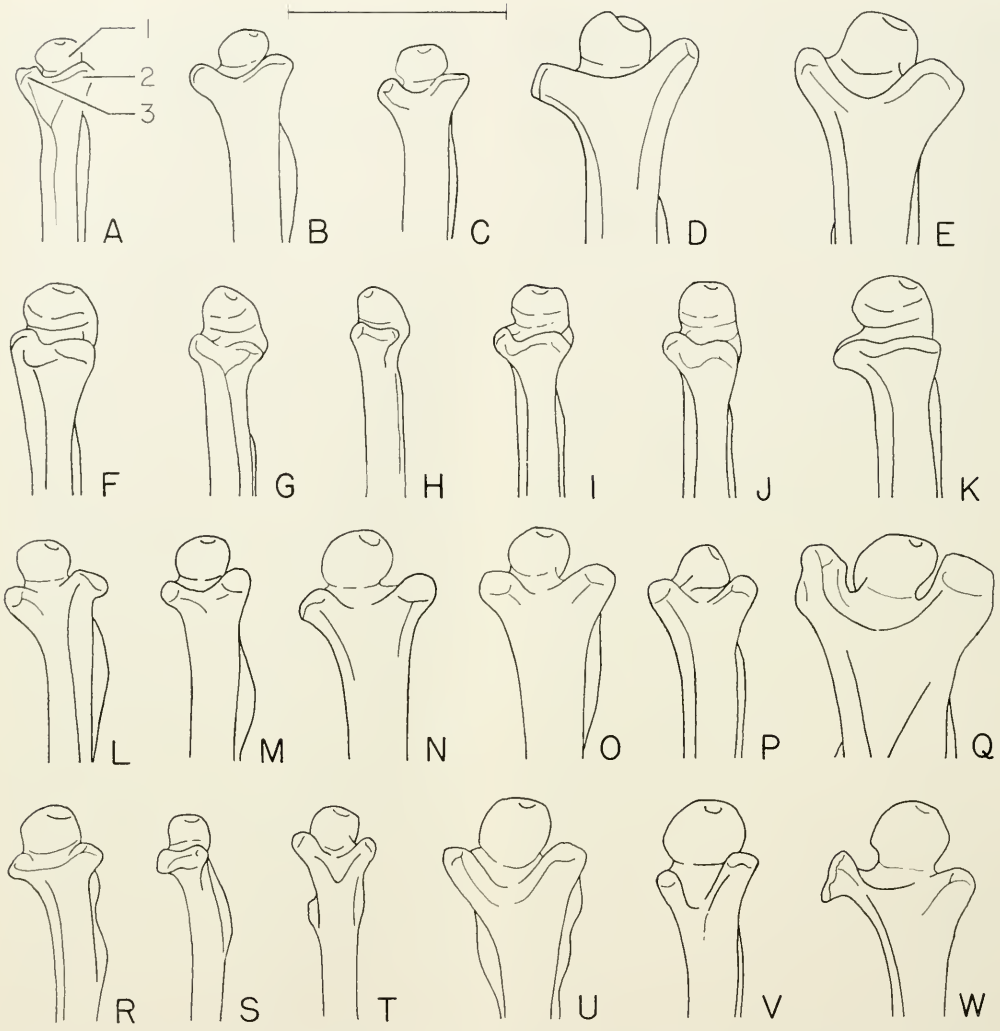


FIGURE 8. Lateral view of the proximal end of the femur of representative New World bats: A, *Rhynchonycteris naso;* B, *Saccopteryx bilineata;* C, *Balantiopteryx plicata;* D, *Diclidurus virgo;* E. *Noctilio labialis;* F, *Pteronotus parnellii;* G, *P. personatus;* H, *P. fuliginosus;* I, *P. davyi;* J, *P. suapurensis;* K, *Mormoops megalophylla;* L, *Micronycteris sylvestris;* M, *Glossophaga soricina;* N, *Carollia perspicillata;* O, *Sturnira lilium;* P, *Artibeus toltecus;* Q, *Desmodus rotundus;* R, *Natalus stramineus;* S, *Furipterus horrens;* T, *Thyroptera tricolor;* U, *Myotis grisescens;* V, *Lasiurus borealis;* W, *Molossus molossus.* The labels on A refer to the following structures mentioned in text: 1, head; 2, lesser trochanter; 3, greater trochanter. See text for discussion of the proximal end of the femur. The line above B and C is 4 mm in length.

the shaft, and extends antero-medially (Fig. 8).

The overall structure of the femur in *Desmodus* (Fig. 8Q) is noteworthy because the bone is laterally compressed and has numerous grooves and ridges (as described by Miller, 1907:176). The lesser and greater trochanters are widely spread and almost equal the head in size and proximal extension. These adaptations apparently relate to the agility of these bats in terrestrial locomotion.

Other interesting modifications are

seen in the genera *Natalus* and *Furipterus* (Fig. 8, R and S) in which both trochanters are somewhat reduced in size. In the vespertilionid genus *Lasiurus* (Fig. 8V), the head is spherical and the greater trochanter is slightly smaller than the lesser trochanter. The molossid bats (Fig. 8W) exhibit a characteristic hook-like projection on the greater trochanter.

The functional significance of the marked differences in the size and shape of the two trochanters observed between mormoopids and other bats is not readily apparent. Muscle groups that are associated with the trochanters play important roles in bracing the hind limb against the lateral pull of the wing membrane during its cycle and may become involved in the forward stride in terrestrial locomotion. Other muscles that originate from the region of the trochanters also control the posture of the hind limb in flight.

Tragus

The ears of the Microchiroptera are complex and usually appear as cone-like horns, directed anteriorly. The ears of the Megachiroptera, on the other hand, resemble those of terrestrial mammals. In addition, the interior of the pinna and the auricular cavity of microchiropteran ears may be furnished with an elaborate array of folds and flaps, the most conspicuous of which is the tragus. Although greatly reduced in size in the molossid bats, the tragus is present in all New World families. It is absent in the Old World family Rhinolophidae (including Hipposideridae).

The tragus is attached just anterior to the external auditory meatus and seems to be situated directly in the path of sound waves that enter the auricular cavity. Griffin (1958:129) noted that the tragus probably does not interfere appreciably with the passage of sound waves to the auditory meatus. Although there is no evidence to support or refute this assumption, it seems highly probable to me that the size, shape, and pubescence of the tragus alter, in some way, the character of these sound waves as they travel through the external ear.

Dobson (1878), Flower and Lydekker (1891), and Miller (1907), among others, commented briefly on the structure of the tragus as it pertained to their taxonomic arrangements. Numerous recent authors, for example Davis (1965: 230) and Peterson (1968:6), have illustrated and described the tragus with reference to differences between species, and I have found it to be a highly reliable character at the familial, generic, and specific levels of classification. Differences at the specific level are manifest in proportion and size, whereas generic and familial affinities are usually reflected in variations in shape.

The tragus of emballonurids is typically a rather small flap of skin that projects laterally into the auricular space. In most cases, it is broad and squared as in *Saccopteryx* (Fig. 9B), but may be erect and bluntly spatulate as in *Rhynchonycteris* and *Peropteryx* (Fig. 9, A and C). The lateral edge (that which projects into the auricular cavity) may be simple, notched, or serrated, and may be naked or clothed with short bristle-like hairs.

In the Noctilionidae (Fig. 9D) the tragus is a slender, pinnately-lobed structure with one finger-like projection on the cranial edge (directed toward the side of the head) and three or four on the lateral edge. Short bristle-like hairs cover most of tragus, which has a small secondary lobe near the base.

Typically, the tragus of phyllostomatids is divided into a main section, usually lanceolate in shape (Fig. 9, F-H), and a secondary oblique lobe near the base on the lateral edge that projects ventrad and posteriorly. Generally, the main support for the tragus is a ridge, which may be heavy to weak and extends along the longitudinal axis of the main section on the cranial side. This ridge causes the central portion of the

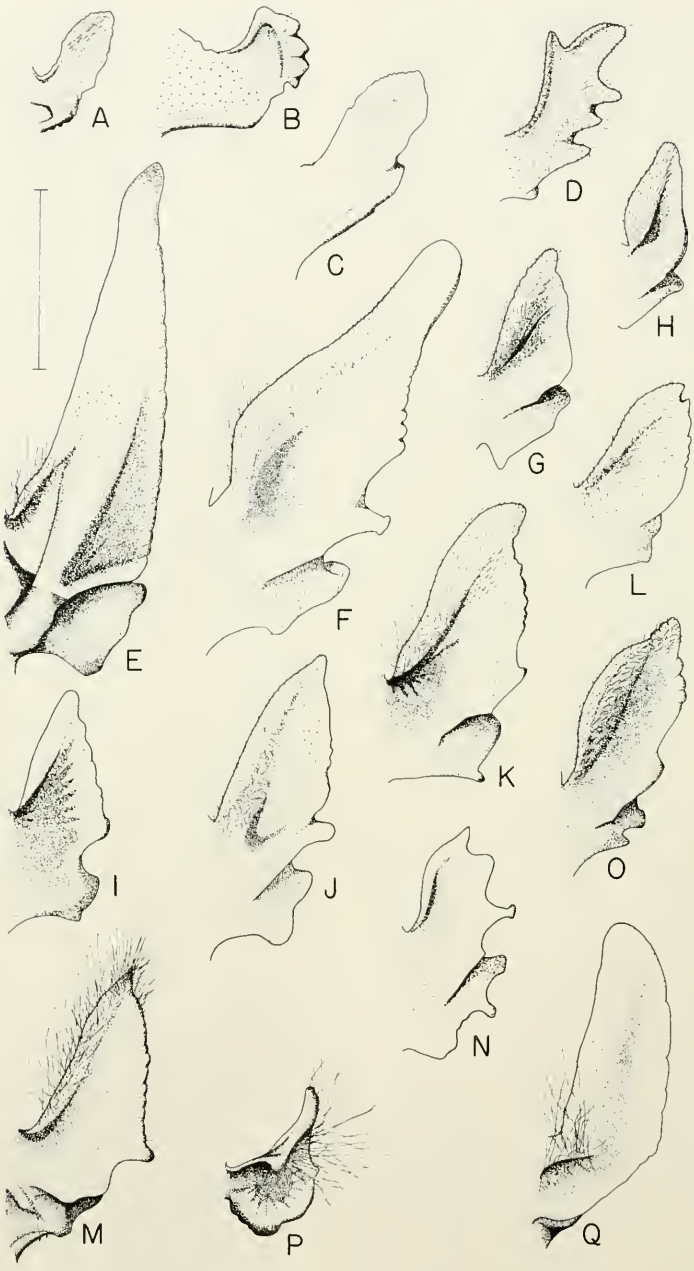


FIGURE 9. Tragus of some representative New World bats: A, *Rhynchonycteris naso;* B, *Saccopteryx bilineata;* C, *Peropteryx macrotis;* D, *Noctilio labialis;* E, *Lonchorhina aurita;* F, *Phyllostomus hastatus;* G, *Glossophaga longirostris;* H, *Lionycteris spurrelli;* I, *Uroderma bilobatum;* J, *Artibeus lituratus;* K, *Carollia perspicillata;* L, *Sturnira lilium;* M, *Desmodus rotundus;* N, *Ametrida centurio;* O, *Phyllonycteris poeyi;* P, *Natalus stramineus;* Q, *Eptesicus fuscus.* See text for discussion of tragus. Line below A is 5 mm in length.

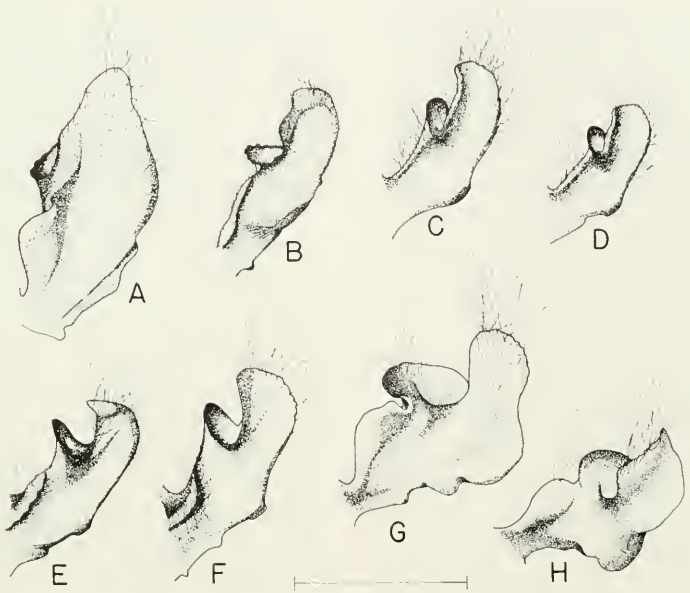


FIGURE 10. The tragus of mormoopids: A, *Pteronotus parnellii;* B, *P. personatus;* C, *P. macleayii;* D, *P. fuliginosus;* E, *P. davyi;* F, *P. suapurensis;* G, *Mormoops megalophylla;* H, *M. blainvillii.* See text for discussion of tragus. Line below G is 5 mm in length.

tragus to be concave, either deep or shallow, depending on the nature of the ridge. The extremely elongated tragus of *Lonchorhina aurita* (Fig. 9E) is strongly convex, rather than concave, and the supporting ridge is absent. The lateral edge of the phyllostomatid tragus may be simple as in the Glossophaginae (Fig. 9, G and H) or notched, serrated, or both (see *Uroderma, Artibeus, Carollia,* and *Sturnira* in Fig. 9, I-L). Pubescence is also variable from completely nude as in *Uroderma* and *Ametrida* (Fig. 9, I and N) to exceedingly hairy as in *Desmodus* (Fig. 9M).

The tragus of members of the Natalidae (Fig. 9P) is curled into a curious cone-like structure, from which many long hairs project. Disc-winged bats (family Thyropteridae, not illustrated) have a tragus that is essentially similar to that of natalids, except that it lacks the long hairs. From the description and illustration given by Husson (1962: 200-201), the tragus of *Furipterus horrens* (family Furipteridae) also seems to resemble that of natalids.

The least variation in shape was observed in the Vespertilionidae. In this group the tragus is usually spatulate (as in *Eptesicus fuscus,* Fig. 9Q), but may be acuminate. Variation observed in this group relates primarily to size. In almost every case, the lateral edge of the tragus is simple or only slightly crenulate, and pubescence, if present, usually is restricted to the basal portion of the structure.

As mentioned above, the tragus of molossids (not illustrated) is greatly reduced in size. In most cases it is little more than an inconspicuous finger-like projection as typified by the genus *Molossus,* but may be relatively large and squared as in the genus *Tadarida.*

Generally speaking, the tragus of the above-mentioned New World families is little more than a simple flap of skin that projects into the auricular cavity. This is also true for those Old

World families that possess a tragus, with the exception of the Myzopodidae, in which the structure is mushroom-shaped (Walker *et al.*, 1964:333).

By comparison, the tragus of the Mormoopidae is considerably different. In this group, there is a rather interesting sequential transition from the simplest, in *Pteronotus parnellii* (Fig. 10A), to the most complex, in *Mormoops megalophylla* and *M. blainvillii* (Fig. 10, G and H). This transition is from a seemingly simple lanceolate tragus to one with a secondary fold of skin that lies at a right angle to the main longitudinal axis of the structure. This secondary fold is barely more than a pocket-like structure in the cranial edge of the tragus in *Pteronotus parnellii* (Fig. 10A). In *Pteronotus macleayii, P. fuliginosus, P. davyi,* and *P. suapurensis* (Fig. 10, C-F), the fold is well developed. In *Pteronotus personatus,* the fold is not so markedly developed, but appears as a cranially oriented shelf (Fig. 10B). Finally, in the genus *Mormoops,* the fold is greatly increased in size and forms the major part of the tragus. Below the secondary fold, the cranial edge of the tragus is swollen and forms a heavy fleshy ridge. The pubescence is variable in this group, but long filamentous hairs are common on the blunt end of the tragus around the edge of the secondary fold, and along the cranial edge below this fold.

Correlative Information from Other Sources

From the foregoing accounts, it is apparent that the family Mormoopidae stands apart in a number of morphological characteristics from the Phyllostomatidae, with which it has been grouped (as a subfamily) in the past. Several noteworthy examples of other differences have appeared in the literature, and these are summarized here as additional evidence of the distinctness of the Mormoopidae in comparison with phyllostomatids and other New World chiropteran families.

Echolocation.—Various aspects of the acoustic orientation in bats have occupied the interest of mammalogists for some time and a wealth of information has accumulated. Most investigations in this regard have been descriptive and have been based on Holarctic bats, principally of the family Vespertilionidae. More recently, echolocation of Neotropical bats has been studied, and some attempts now are being made to understand better the functional and behavioral aspects of echolocation (Grummon and Novick, 1963; Novick, 1963b, 1965; and Novick and Vaisnys, 1964). Several Neotropical species of the Phyllostomatidae (here including the mormoopid genera) and *Desmodus* were first examined by Griffin and Novick (1955). More recently, with the advent of better high-frequency sound-detecting equipment, Griffin (1958), Griffin and Grinnell (1958), Grinnell and Griffin (1958), and Novick (1958, 1962, 1963a) have contributed greatly to our knowledge of echolocating systems in Neotropical bats.

The high-frequency sound emissions of several mormoopid species—*Pteronotus parnellii, personatus,* and *suapurensis*—were recorded and analyzed by Griffin and Novick (1955). It is noteworthy that these authors found that mormoopids emitted high-frequency sounds that more closely resembled those emitted by emballonurids than those of "other" phyllostomatids. The pulses were elicited orally by mormoopids rather than nasally as in phyllostomatids, were long and relatively intense, and lacked the progressive frequency modulation observed in vespertilionids, molossids, and noctilionids. The range of the predominate frequency was observed between 20 and 100 kilocycles. By comparison, phyllostomatids emitted shorter pulses of intermediate intensity with a rather simple frequency spectrum (predominant frequency 12 to

50 kilocycles) and harmonics of variable amplitudes. These same results were again obtained by Novick (1958).

Novick (1963a) re-examined the acoustic orientation pulses of several phyllostomatids (including desmodontines) and the mormoopid species *Pteronotus parnellii, personatus,* and *davyi.* His findings were generally consistent with those obtained by Griffin and Novick (1955), who had used somewhat less sophisticated equipment. In this paper, Novick (1963a:47) noted that *parnellii* was strikingly different from the other mormoopid genera studied, as well as phyllostomatids in general. The particular features of the pulses that seemed most significant to him were their unusually long duration and slight degree of frequency modulation. On the other hand, *personatus* and *davyi* elicited similar pulses of shorter duration and with gradual frequency modulation, dropping from beginning to end. All three species seemed to have two harmonics and *personatus* frequently produced a third overtone, which Novick (1963a:48) thought might be significant.

The members of the family Mormoopidae appear to differ markedly from phyllostomatids judging from the results of studies concerning chiropteran echolocation thus far conducted. Dr. Novick (personal communication) stated that he had doubted the relationship of the "Chilonycterinae" to the Phyllostomatidae for some time based on their behavior in locomotion, feeding in captivity, and roosting, as well as the marked differences in frequency pattern, intensity, and other features of their sonar design. Information concerning the acoustic orientation of *Mormoops* is not yet available.

Hair structure.—The scales of chiropteran hair were examined microscopically as early as 1875 by J. D. Macdonald, the results being published as a footnote in Dobson (1875:355-356). More recently, Benedict (1957) examined numerous representative genera of bats in this regard. She was concerned not only with scalation, but also filament length, distribution of pigmentation, structure of the medulla, and differentiation of the pelage into "overhair" and "underhair." Benedict noted that "chilonycterines" have scales arranged in a simple annular fashion, whereas phyllostomatids have scales arranged in an alternating fashion, but she found no other peculiarities separating the two groups.

I have examined, in a cursory manner, whole-mount slides of hair from some representatives of New World families. The mormoopids (except *Mormoops*) have the coronal scales arranged in an annular fashion. Perhaps a better description would state that these scales approach the unequal hastate type as described by Benedict (1957:290). Scales of *Mormoops* hair, by comparison, are clearly unequal hastate and have the terminal edge markedly serrated. Although no marked differences in hair structure distinguish mormoopids from phyllostomatids, some interesting features do exist that merit further investigation.

Studies of karyotypes.—Some useful information concerning the phylogenetic relationships among the New World Chiroptera has been obtained recently from studies of karyotypes (see especially Baker and Patton, 1967, and Baker, 1967, 1970).

Baker (1967) examined many phyllostomatid genera representing nearly every subfamily except the Phyllonycterinae and Desmondontinae; later, Forman *et al.* (1968) found that karyotype data generally supported the inclusion of the vampires as a subfamily of the Phyllostomatidae. In this paper, Baker examined the karyotypes of *Pteronotus parnellii, personatus,* and *davyi* and found that all three species were indistinguishable. The karyotype of *Mormoops megalophylla* was first reported by Baker and Hsu (1970).

The mormoopids examined have a rather high number of metacentric pairs (11) as compared with the phyllostomatids examined (one to eight, mean six). Mormoopids also have one pair of submetacentrics (none to seven in phyllostomatids), no subtelocentric pairs (none to six in phyllostomatids), and six acrocentric pairs (the majority of phyllostomatids examined had none). The diploid number in the four mormoopid species examined was 38 with a fundamental number (total number of chromosome arms) of 60 (62 in *Mormoops megalophylla*). In phyllostomatids, the diploid number averaged 29 (16-46) and the fundamental number averaged 52 (24-68).

From this information, Forman *et al.* (1968) concluded that the "chilonycterines" were unique karyotypically among the Phyllostomatidae and that they were sufficiently distinct to merit at least subfamilial status.

Histological aspects of facial glands. —The histological aspects of the glands of the facial regions of North American bats have been reported on by Werner *et al.* (1950), Dalquest *et al.* (1952), Werner and Dalquest (1952), and Dalquest and Werner (1954). The last paper is mostly a summary of previous work and the systematic implications of this research. Numerous genera, representing all New World families except the Noctilionidae, Furipteridae, and Thyropteridae, were examined. Dalquest and Werner (1954) found that each of the families considered could be adequately characterized and identified solely on the basis of the histology of the facial region. Their results conform closely to the existing taxonomic arrangement of bats, excepting that they recognized the mormoopids as a separate family which they referred to as the "Chilonycteridae." Their reasons for this action, however, were not made exactly clear.

The mormoopid genera examined by Dalquest and Werner (1954) were *Pteronotus parnellii, P. davyi,* and *Mormoops megalophylla,* all of which were found to be histologically similar with regard to the facial region, except that *Mormoops megalophylla* was observed to have submaxillary glands composed of serous cells rather than of the mucous type commonly found in other bats. Molossids also were found to have serous cells in the submaxillary glands (as well as in the sublingual glands). None of the other New World families exhibited serous sublingual glands.

These authors also found that the New World families could be grouped by the presence or absence of the sudoriferous glands in the facial region. These glands were present in the Emballonuridae, Vespertilionidae, and Natalidae. Sudoriferous glands were absent from the facial area in the "Chilonycteridae," Phyllostomatidae, Desmodontidae, and Molossidae. The presence or absence of these glands was thought to be conservative and consistent among New World groups. Families that possessed such glands were presumed to be primitive and more closely related to one another than to groups that did not have these glands. Consequently, Dalquest and Werner suggested a phylogenetic arrangement that reflected these two groupings.

Selected ectoparasites. — Although several groups of ectoparasites are found on bats, only a few groups parasitize bats exclusively. Three of these so-called "obligate" parasite groups are the Spinturnicidae (Acarina), Nycteribiidae (Diptera), and Streblidae (Diptera). In the past, mammalogists have been reluctant to accept phylogenetic information based on host-parasite relationships, particularly those involving ectoparasites. Part of this reluctance evidently stems from the fact that few careful collections of ectoparasites have been made. In the Chiroptera, ecological factors are of paramount concern, especially when two or more host species come into close physical proximity at

feeding and roosting sites. This, coupled with the fact that some of the ectoparasites of bats pass stages of their life history away from the host, has led to caution concerning assumptions of host specificity and phylogenetic implications based on taxonomic concordance of parasites and their hosts. Host specificity is discussed in some detail by Wenzel and Tipton (1967).

At least one group of chiropteran ectoparasites seems to be relatively host-specific—the wing mites of the family Spinturnicidae (Acarina, Mesostigmata). The life history of these mites has been modified by the reduction of nymphal stages and the development of ovoviviparity (Baer, 1952, and Rudnick, 1960). These adaptations make this group a reasonable one to turn to for some indication of phylogeny within the Chiroptera.

According to Machado-Allison (1967: 224) mites of the family Spinturnicidae are intimately involved with the Chiropteran family Phyllostomatidae, being found on all except the endemic Antillean subfamily Phyllonyeterinae. Earlier, Machado-Allison (1967:225) suggested the inclusion of the vampire bats in the Phyllostomatidae based on the occurrence of the spinturnicid species *Periglischurus herrerai* on *Desmodus rotundus*. Other species of this genus have been reported from *Noctilio leporinus* (Noctilionidae) and *Natalus stramineus* (Natalidae) by Furman (1966). Recently, Machado-Allison (1965b) reviewed the species of the spinturnicid genus *Periglischurus* Kolenati. The spinturnicids that he encountered on bats of the species *Pteronotus parnellii* were so distinct morphologically that he (1965a) named them as a new genus and species, *Cameronieta thomasi*. Machado-Allison (personal communication) also thinks that the species *Periglischurus strandtmanni*, known from *Mormoops megalophylla*, is referable to his genus *Cameronieta*.

In his review of the spinturnicid mites of Panamá, Furman (1966:166) placed the genus *Cameronieta* Machado-Allison in synonymy under *Periglischurus*, based on a close resemblance between *C. thomasi* and *P. elongatus* Furman, 1966 (known from *Pteronotus parnellii* and *P. suapurensis*). Furman (1966) regarded the species *thomasi* and *elongatus* as distinct, pending further investigation to demonstrate his hypothesis for the existence of heteromorphic females; he considered both species close relatives of *P. strandtmanni*. The resolution of the *Cameronieta-Periglischurus* problem remains in the hands of the acarologists. The point to be made is that apparently the spinturnicid mites found on mormoopid bats are, as a group, distinct from those found on phyllostomatids, implying distinctiveness in the bats as well.

The batflies of the family Streblidae are not as host specific as are spinturnicids, but they also suggest some interesting relationships. Wenzel *et al.* (1966), reporting on the streblids from Panamá, indicated (p. 652) that representatives of the streblid subfamily Nycterophiliinae *(Trichobius* and *Nycterophilia)* occur primarily on the "Chilonycterinae" and Natalidae, but also are known from *Platalina* (Glossophaginae) and *Macrotus* (Phyllostominae). Wenzel *et al.* (1966) continued by stating: "The host distribution of these groups of *Trichobius* and *Nycterophilia* support the view of Dalquest and Werner (1954) and de la Torre (1961) that the Chilonycterinae should be regarded as a separate family of Vespertilionoidea rather than as a subfamily of the Phyllostomatidae."

Brain size. — Recently, Findley (1969), in a paper concerned with brain size of various bats, recorded some quantitative and qualitative differences between mormoopids and phyllostomatids. Relative brain size was found to be smaller in the former. Additionally, he noted that mormoopids are similar

to molossids and lasiurines in that the cerebral hemispheres are relatively small, the cerebelli relatively large, and that the midbrain is visible between these two areas. The cerebral hemispheres apparently are large in many phyllostomatids. As noted by Findley, brain size alone probably indicates little concerning the biology and relationships of bats; enlargement of particular cerebral regions, however, may have taxonomic significance correlated with other morphological features.

Immunologic relations.—In a recent paper Gerber and Leone (1971) reported on immunologic comparisons of the sera of certain phyllostomatid bats. On the basis of turbidimetric tests, they found *Pteronotus suapurensis* to differ appreciably from other species of phyllostomatids *(Glossophaga soricina, Carollia perspicillata, Artibeus jamaicensis,* and *Desmodus rotundus*). This distinctness appeared to be almost as great as that demonstrated by representatives of the Vespertilionidae and Molossidae.

PHYLOGENETIC RELATIONSHIPS OF THE MORMOOPIDAE

The student of chiropteran evolution is faced with one of the largest and most diverse groups of mammals and yet one of the poorest known in terms of past history. Bat fossils are relatively common in some fissure faunas of Europe, but have not been reported in detail. Some of these remains (all representing fully evolved bats) have been recovered from deposits as far back as early Eocene. In the New World, only a few supposedly ancient chiropteran fossils were known until recently (the genera *Picrodus* and *Zanycteris* from the North American Paleocene). Simpson (1945: 178, 180) regarded these as "possible" phyllostomatid bats, but assigned them to Insectivora, *incertae sedis.* McKenna (1967:608) placed these two genera in the Omomyoidea, *incertae sedis.*

Jepson (1966, 1970) described *Icaronycteris index* from the early Eocene (Green River formation) of Wyoming, and Savage (1951) described *Notonycteris magdalenensis* from the late Miocene of the Neotropical La Venta Fauna of Colombia. Although *Notonycteris* is not as well preserved as *Icaronycteris,* it is clearly an early representative of the Neotropical family Phyllostomatidae. The majority of the remaining fossil bats in the New World are of much later age, and most are members of Recent (or closely related) species.

As mentioned earlier, there is a reasonably good array of fossil chiropteran material from the early Cenozoic era of the Old World. Notable among these are *Archaeonycteris* Revilliod and *Palaeochiropteryx* Revilliod from the lignite beds (Messel, early Eocene) near Darmstadt, Austria. These are the earliest known bats in the Old World assemblage. Members of the Rhinolophidae *(Pseudorhinolophus)* are found as early as middle Eocene, and emballonurids *(Vespertiliavus),* vespertilionids *(Nycterobius),* and molossids (fragment of proximal end of humerus, genus indeterminable) occur in the Quercy fauna (Eocene-Oligocene border). These early bats are not noticeably "primitive" and resemble modern species in many features. Detailed accounts of these Old World fossil bats were given by Revilliod (1917a, 1917b, 1920, 1922).

Schlosser (1911:72) described *Provampyrus orientalis* based on a right humerus from the Fayum beds (early Oligocene) of Egypt. He assigned this fossil bat to the family Phyllostomatidae because this humerus seemed to resemble that of "*Vampyrus auritus*" and "*Stenoderma undatum.*" Schlosser (1911: pl. 13) illustrated this bone, which he reported to be 49 mm in length. The proximal end clearly is not that of a phyllostomatid, the greater tuberosity being long and extending well beyond the rounded head. Little can be deter-

mined from the distal end as to structure of the medial process, because it is obscured. In my opinion, this species is best referred tentatively to the Megadermatidae.

Because of the meager fossil record, mammalogists who have studied the evolution of bats have relied on resemblances among representatives of living groups. The task of constructing a workable phylogeny is further complicated by the fact that little is known as to how the majority of the features used to distinguish groups of bats relate to chiropteran evolution. Much of our current conception of chiropteran phylogeny dates back to Dobson (1875), Winge (1892), and Miller (1907). The arrangements of these workers primarily reflect the number and kinds of teeth in the dental arcade and the configuration of the cusps on the molar teeth.

The relationships of the Mormoopidae are not readily apparent; mormoopids having been shuffled between the Noctilionidae and Phyllostomatidae. Dobson (1875:353) thought that *Noctilio* connected the Emballonuridae with the Phyllostomatidae through the "Lobostominae" (= Mormoopidae). In order to clarify the relationships within the Chiroptera, Simpson (1945) grouped Miller's (1907) families into superfamilial units based on Winge's (1892) families. As a result, the Noctilionidae was grouped along with the Rhinopomatidae and Emballonuridae in the superfamily Emballonuroidea. The mormoopids were carried as a subfamily of the Phyllostomatidae into the Phyllostomatoidea along with the vampire bats. All of the remaining New World families were placed in the Vespertilionoidea.

Judging by the proximal and distal portions of the humerus, the proximal end of the femur, and the tragus, the mormoopids are quite distinct from the Phyllostomatidae. Using these same criteria, the Mormoopidae bears little resemblance to the Noctilionidae or Emballonuridae. Yet in some other respects the Mormoopidae, Noctilionidae, and Phyllostomatidae resemble one another more than they resemble any other New World group. The premaxillary bones are complete and solidly fused to the maxillary and palatine bones; the three families are probably the only New World bats in which an os penis is characteristically absent, and the upper incisors usually are strong, heavy teeth, although these are secondarily modified or lost in some phyllostomatids. Unlike the New World emballonurids, there is a marked sella turcica (cup-like depression in the floor of the braincase that holds the hypophysis) behind which there is a prominent clinoid plate (both are minimally developed, but present, in the Noctilionidae). In the Mormoopidae and Phyllostomatidae, the posterior clinoid processes (viewed through the *foramen magnum*) usually are long and have small terminal knobs. The foramina ovale are similarly situated in the three families; the foramen may be hidden beneath an anteriorly projecting ridge of the posterior sphenoid (alisphenoid and basisphenoid complex) or tightly squeezed against the auditory bulla in other groups of bats. For the most part, the basicranial region of these bats is relatively simple, lacking any indication of the extremely deep, sometimes partitioned, basisphenoidal pits found in emballonurids, the function of which remains unknown.

In all three families, there is a curious array of wart-like bumps and ridges on the central portion of the lower lip and chin regions. Labial ornamentation is rather simple in *Noctilio*, consisting of a central tubercular pad on the lower lip surrounded by a secondary transverse ridge that communicates with the lower lip via two connecting ridges. In the Mormoopidae, this region is much more complicated. The central tubercular pad of *Pteronotus* is more or less unchanged, but the lower lip is expanded and plate-like with many con-

centric rows of small bumps that surround the central tubercle. This region in *Mormoops* is extremely complicated in that the central tubercle is enlarged with a flat, shield-like plate, covered with many wart-like bumps, that extend anteriorly from the tubercle. Beneath this plate, the notched lower lip unfurls; as in *Noctilio,* there is a secondary transverse ridge below the lower lip. The lip pad of phyllostomatids is usually a triangular pad that may be simple or may possess several concentric rows of wart-like bumps. These structures are absent in all other New World bats.

Despite the above-mentioned similarities between the mormoopids, noctilionids, and phyllostomatids, there are a number of other features to be considered. Both Noctilionidae and Mormoopidae, for example, have characteristically long calcars that support the posterior half of the uropatagium and that extend considerably farther caudad than do the feet. The posterior portion of the uropatagium is usually flexed forward beneath the proximal part; this characteristic posture is never observed in phyllostomatids. Unlike phyllostomatids, several of the distal caudal vertebrae protrude as a "free tail" from the dorsal surface of the uropatagium. (In the Phyllostomatidae the "free" segment of the tail, if present, usually involves only the last or last two caudal vertebrae.) In the above respects, the Noctilionidae and Mormoopidae resemble emballonurids.

The wing membrane attaches relatively high on the side of the body in both mormoopids and noctilionids. Some members of the Phyllostomatinae, probably the most primitive or generalized subfamily of the Phyllostomatidae, also share this high wing attachment. Generally, the morphology of the phallus of mormoopids and noctilionids is similar, in contrast to that of phyllostomatids. In the latter family, the glans is usually a prominent and knob-like structure, whereas in members of the other two families the glans is fan-shaped with many intricate longitudinal folds and grooves. Also, in these two the clitoris of the female has an acute, and not infrequently long, pendant tip.

As regards the dentition of the three families, it is difficult to make an accurate evaluation. The dental arcade of most phyllostomatids has been modified and reduced. The characteristic dilambdodont molar is retained, more or less unchanged, in the subfamily Phyllostomatinae (extremely modified in other phyllostomatids), Mormoopidae, and Noctilionidae.

Judgements as to the phylogeny and evolution of major groups are therefore largely intuitive. It seems to have been generally agreed that the majority of the Microchiroptera originated in the Old World; New World groups presumably evolved from Old World migrants. The chiropteran fauna of the New World comprises several endemic (and possibly autochthonous) groups, among which are the Mormoopidae, Noctilionidae, and Phyllostomatidae. In addition, the New World and the Old World share several cosmopolitan families—Emballonuridae, Vespertilionidae, and Molossidae. The fact that vespertilionids and molossids have their greatest diversity in the Old World and the fact that emballonurids are represented there by a fossil genus of Eocene or Oligocene age seems to suggest that the center of origin and dispersal of these families also was there. This assumption, coupled with the generally accepted idea that microchiropteran bats evolved from an emballonuroid-like ancestor, suggests that mormoopids, noctilionids, and phyllostomatids were derived from an Old World, emballonurid migrant(s).

The fossil record of bats, although scanty, does yield several key points regarding the progression of chiropteran evolution. By Eocene times, there was a world-wide group of fully evolved bats, represented in the New World by *Icaronycteris index* and in the Old

World by *Archaeonycteris* and *Palaeochiropteryx*. These early bats were indeed primitive, not only in number and kinds of teeth and dilambdodont molars, but also in many features of the posteranial skeleton. The primitive nature of the humerus of *Archaeonycteris* and *Palaeochiropteryx* is illustrated by the broad medial process, simple distal articular surface, short (not extended proximally) greater tuberosity, and rounded head. (These features cannot be readily observed in the illustrations of *I. index*—see Jepsen 1966:1334.) In addition, the pelvic girdle, femur, and long tail contribute to the primitive appearance of these ancient bats. Do they represent a worldwide grade in the evolution of chiropterans or merely several unsuccessful lines from the earliest ancestors of chiropterans?

In consideration of the phylogeny of New World bats, especially mormoopids, noctilionids, and phyllostomatids, the above propositions are of paramount importance. The discovery of *Notonycteris* indicates that phyllostomatids were well established in an evolutionary sense by the Miocene. It is also apparent that the oldest emballonurids from the Quercy fauna (Eocene-Oligocene of the Old World) were similar to modern species of that group. The time involved in the differentiation of the phyllostomatids from the emballonurid-like ancestor (if this were the case) seems to shift unduly the whole evolutionary sequence of bats as well as placental mammals to a much earlier, yet undocumented age. It seems reasonable to suppose that a "paleochiropteran" grade existed in both the Old World and the New World during middle to late Paleocene times. The importance of this group is that it could provide a plausible ancestor, both on the basis of age and generalized structure, for the Noctilionidae, Mormoopidae, and Phyllostomatidae, assuming that these three families are intimately related.

For the reasons outlined above, I think that the Mormoopidae, Noctilionidae, and Phyllostomatidae represent three distinct families that probably had a common ancestral line. It seems premature at this time to place all three in the superfamily Phyllostomatoidea, although further investigation may show this to be the proper arrangement. Furthermore, they may represent a truly autochthonous lineage that evolved from a paleochiropteran grade in the New World, although there is no clear evidence for or against this hypothesis. In addition, the Mormoopidae seems to be more closely related to noctilionids than to phyllostomatids, and in many respects the Noctilionidae appears to be the least specialized of the three families.

SYSTEMATIC ACCOUNTS

Family Mormoopidae Saussure

Mormoopsins Saussure, 1860, Rev. Mag. Zool., ser. 2, 12:286, July.

Mormopes Peters, 1865, Monatsber. k. preuss. Akad. Wiss., Berlin, p. 257.

Mormopsina Gray, 1866, Ann. Mag. Nat. Hist., ser. 3, 17:93, February.

Phyllodiana Gray, 1866, Ann. Mag. Nat. Hist., ser. 3, 17:93, February.

Lobostominae Dobson, 1875, Ann. Mag. Nat. Hist., ser. 4, 16:350, November.

Chilonycteriinae Flower and Lydekker, 1892, An introducton to the study of Mammals living and extinct, p. 672.

Mormopinae Trouessart, 1897, Catalogus mammalium tam viventium quam fossilium, 1:150.

Mormoopinae Rehn, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54:162, June 11.

Type genus.—Mormoops blainvillii Leach, 1821.

Geographic distribution. — New World, from southern Arizona and southern Texas south through México (including Baja California and the Yucatan Peninsula), British Honduras, Central America, and South America (including Trinidad) to Mato Grosso, Brasil; generally restricted to tropical

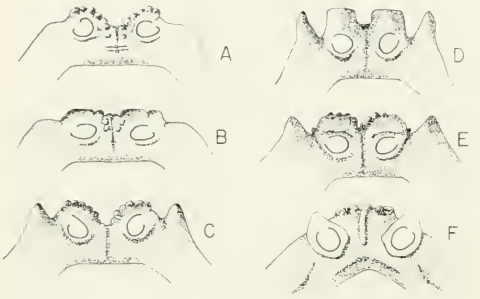


FIGURE 11. Labio-nasal region of six mormoopids: A, *Pteronotus parnellii;* B, *P. personatus;* C, *P. davyi;* D, *P. macleayii;* E, *P. fuliginosus;* F, *Mormoops megalophylla.* See text for discussion.

habitats below 3000 meters. Endemic species or races also are found on the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) and in the Dutch West Indies. One species, *Pteronotus davyi,* is known from the Lesser Antillean islands of Grenada, Dominica, Marie Galante (off Guadeloupe), and Martinique.

Description. — Mustached bats, naked-backed bats, and ghost-faced bats of the family Mormoopidae range in size from the small *Pteronotus fuliginosus* (forearm length 35-40) to the large *P. parnellii* (forearm length 54-65). Unlike the phyllostomatids, with which they have been grouped in the past, the mormoopids do not possess a nose-leaf. Instead, the lips have been expanded and ornamented with various flaps and folds that form a "funnel" into the oral cavity when the mouth is opened. Short bristle-like hairs surround this "funnel" and may act to direct airflow toward the scoop-like mouth in the same manner as in some insectivorous birds. The nostrils have been incorporated into the expanded upper lip; above and between them are various bumps and ridges that, along with the region immediately lateral to the nostrils, form a labio-nasal plate. The shape of this plate is useful in distinguishing taxa of this family (Fig. 11 and discussion beyond).

The rostrum is relatively long in the genus *Pteronotus,* but short and upturned in *Mormoops.* The pinnae of the ears are funnel-shaped, with a distal portion that may be long and lanceolate *(Pteronotus),* or extremely short and rounded *(Mormoops).* The medial edge of the distal portion of the pinna may be simple, but is serrated in several species. The lower edge of the pinna is always confluent with a ridge that extends along the lower lip. Dorsally the ears may be weakly connected by two low and inconspicuous ridges that join on the rostrum and form a prominent rostral tubercle as in the subgenera *Phyllodia* and *Chilonycteris;* both ridges are extremely inconspicuous in the subgenus *Pteronotus* and the rostral tubercle is reduced or absent. In the genus *Mormoops,* the ears are united by two prominent bands that meet on top of the rostrum and form a high, V-shaped tubercle. The tragus is complex (Fig. 10), and the eyes are small and inconspicuous as compared with the large and prominent eyes of phyllostomatids.

The wing membrane is variously attached to the side of the body. In the subgenus *Pteronotus,* the wing membranes meet and fuse on the dorsal midline, giving these bats a naked-backed appearance, but the attachment is somewhat lower on the side in the other mormoopids. The wing membrane and extensive uropatagium attach to the leg by way of a weak to strong ligament, which may be tightly bound to, or entirely free from, the tibia. The foot is normal and the calcar is long and usually flexed forward against the tibia. A tail is always present and approximately half of the distal portion protrudes dorsally from the uropatagium.

The pelage of the mormoopids is short, fine, and densely distributed over the body. Bats of this family were previously thought to possess two distinct color phases, but as will be shown later, these phases appear to be seasonal. It is noteworthy that the naked-backed bats possess a thick, long pelage beneath the dorsally fused wing membranes.

The rostrum and braincase are well defined regions of the mormoopid cranium; they are more or less in the same plane in the genus *Pteronotus*, but the rostrum is markedly up-turned, resulting in an abruptly rising forehead in *Mormoops* (Fig. 37). The premaxillaries are complete and solidly fused. Although some teeth are noticeably reduced in size in certain species, the dental formula for all mormoopids is i 2/2, c 1/1, p 2/3, m 3/3 = 34. The upper molars have a virtually unmodified dilambdodont cusp pattern and the last upper premolar is only slightly molariform. The upper incisors may be heavy, nearly peg-like, and possess a distinct lingual heel, or they may be thin and blade-like (without lingual heel); usually the inner pair are noticeably bifurcate.

Post-cranial features of these bats have been discussed. The proximal end of the humerus is characterized by an elliptical head that is somewhat canted toward the greater tuberosity. Both tuberosities equal the head of the humerus in proximal extension and there appears to be no special relationship between the humerus and the scapula. However, the supraglenoid fossa is well developed and, along with the supraglenoid process, forms an effective locking mechanism. Distally the capitulum and trochlea are well developed in the genus *Pteronotus*; in *Mormoops* the central portion of the capitulum is reduced in size, probably to reinforce the hinge-like elbow joint. A medial process is present and has a well-developed spinous process that is involved in the automatic control of the distal segment of the wing. The olecranon portion of the ulna is strongly developed in *Mormoops*, but markedly reduced in *Pteronotus*. The greater and lesser trochanters of the proximal end of the femur are greatly reduced and located close to the longitudinal axis; the head of the femur is spherical and directed craniad.

Generic Analysis

The species of mormoopid bats have been fairly well defined. However, in the past, as many as four genera, *Phyllodia, Chilonycteris, Pteronotus*, and *Mormoops*, have been recognized (Gray, 1866a:93); also as few as two have been recognized—*Chilonycteris* and *Mormoops* (Dobson, 1878:447), and *Pteronotus* and *Mormoops* (Burt and Stirton, 1961: 25). Miller (1907:119-121) assigned mormoopids to three genera, *Chilonycteris, Pteronotus*, and *Mormoops*. For the most part, these classifications seem to have been primarily founded on two characteristics—the shape of the cranium (more or less normal in *Pteronotus* and *Chilonycteris* and curiously flexed in *Mormoops*) and the fusion of the wing membrane on the back (fused in *Pteronotus* and not fused in *Chilonycteris*). Burt and Stirton (1961:25), in relegating *Chilonycteris* to synonymy under *Pteronotus*, considered the dorsal fusion of the wing membrane to be of no more than specific value.

In constructing a classification of the Mormoopidae, I have attempted to delimit the "natural groups" within the family by using as many characteristics as possible. Close examination of cranial and external features of these bats seemed to indicate the existence of at least three, and possibly four, taxonomic units within the family. While some of these features could be expressed purely by linear dimension, others were more subtle, being proportional or qualitative in nature.

In order to quantify and correlate the observed variation in the cranial and external characters, I took advantage of the multivariate comparisons and correlations offered by techniques of numerical taxonomy. All computations were carried out using the NT-SYS system of computer programs (developed by F. James Rohlf with assistance of John Kishpaugh and Ron Bartcher) on the GE 635 computer at The University of Kansas Computation Center. My first

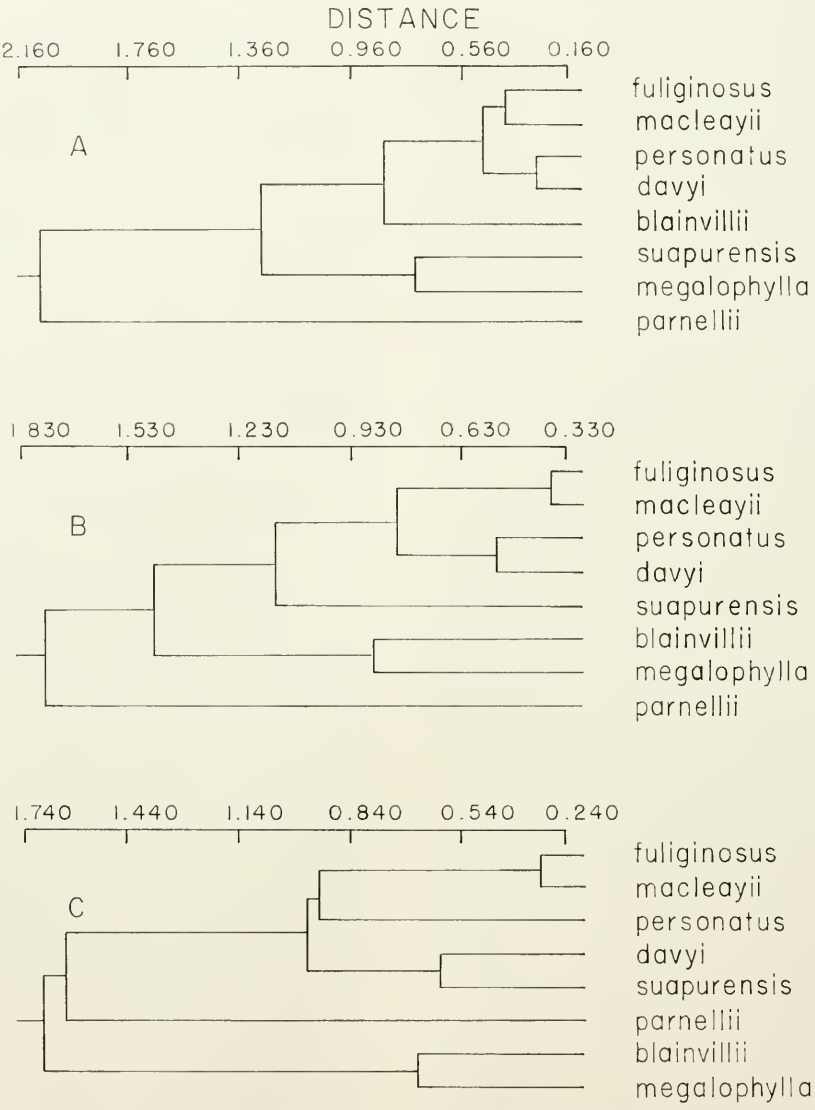
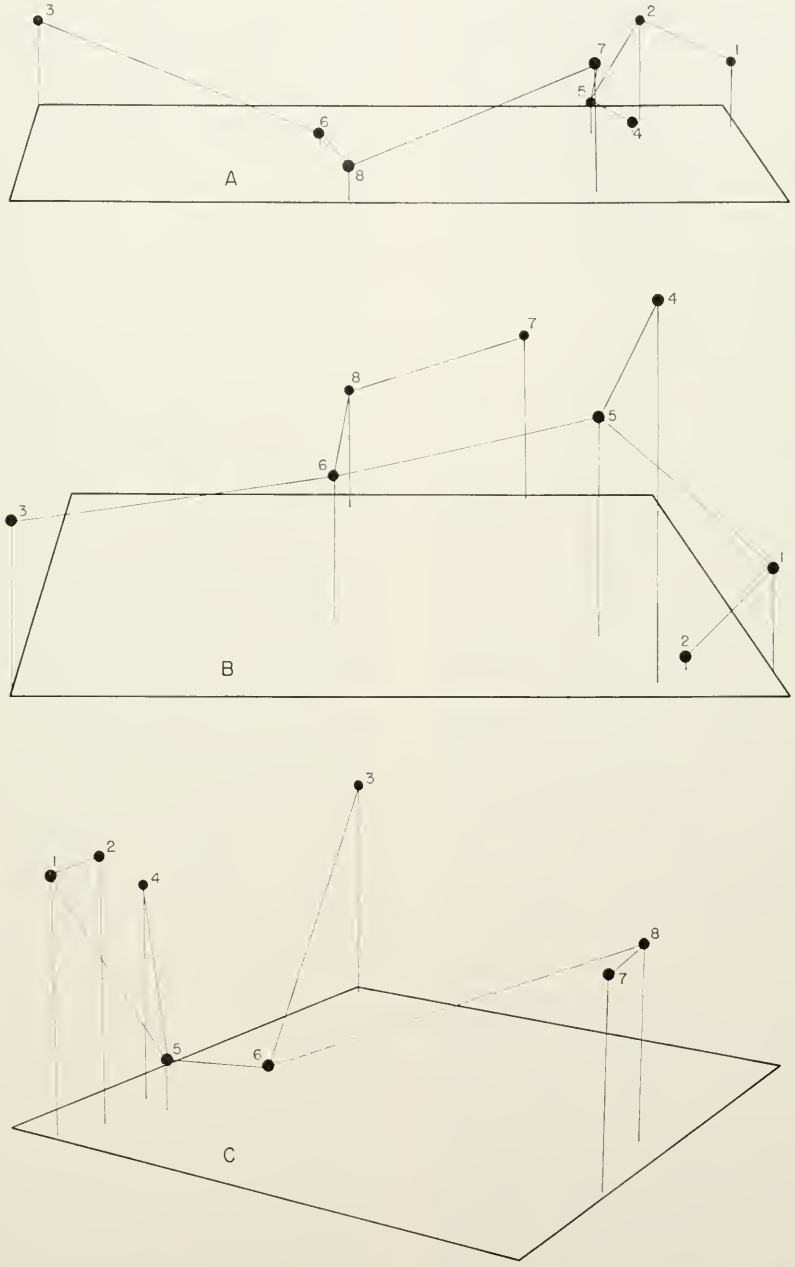


FIGURE 12. Distance phenograms of mormoopid species based on an unweighted pair group method of cluster analysis using arithmetic averages (UPGMA, see Sokal and Sneath, 1963:182-185) computed from distance matrices on standardized characters: A, length of forearm and 11 selected cranial measurements; B, 10 selected cranial angles (Fig. 2) plus those parameters in A; and C, 20 multistate characters in addition to the dimensions used in A and B. The cophenetic correlation coefficient for these three phenograms are 0.906, 0.881, and 0.938, respectively. Scales of distances are located above their respective phenogram.

FIGURE 13. Three-dimensional models of the projections of mormoopid bats onto the first three principal components based on correlations among 12, 22, and 42 characters; A, B, and C, respectively (see Rohlf, 1967 and 1968, for a discussion of 3-D models). The taxa are identified as follows: 1, *fuliginosus;*



2, *macleayii;* 3, *parnellii;* 4, *personatus;* 5, *davyi;* 6, *suapurensis;* 7, *blainvillii;* 8, *megalophylla.* These models represent a somewhat less distorted summary view of the phenetic relationships shown in the distance phenograms (Fig. 12, A-C). Horizontal lines between "balls" illustrate the connections for the shortest simply connected network in *n*-dimensional (character) space projected onto each model (see Kruskal, 1956, and Cavalli-Sforza and Edwards, 1967). The first three factors of the principal components analyses here illustrated account for 98.12, 95.22, and 89.59 per cent of the variation in A, B, and C, respectively. See text for discussion.

attempt to classify the mormoopids incorporated only 11 selected cranial measurements and the length of the forearm (see Methods). My purpose in doing this was to determine what, if anything, these parameters contributed to the classification at the generic level. Figures 12 and 13 show the results of this analysis. As was expected, size alone was the single most influential aspect in this test. In figure 12A species are arranged in the phenogram from the smallest *(fuliginosus)* at the top to the largest *(parnellii)* on the bottom. The cophenetic correlation for this phenogram was 0.906. It is interesting to note that the species of nearly equal size *(davyi and blainvillii, suapurensis* and *megalophylla)* were set off together. The effect of size also is apparent in the three-dimensional projection (Fig. 13A), especially along the *X* axis, which accounted for 82.14 per cent of the trace. Only 13.28 per cent of the trace was expressed on the *Y* axis and 2.71 per cent on the Z axis. Therefore, linear dimension alone, as represented by the cranial and external measurements employed in this study, was found to be of minimal value in classifying the mormoopids at the generic level.

My next concern was to introduce shape as a parameter into the analysis along with the above-mentioned external and cranial dimensions. A representation of shape was obtained by measuring 10 selected cranial angles (see Methods). The results of this analysis (Figs. 12B and 13B) were somewhat more consistent with *a priori* estimates of the resemblances. Again, *parnellii* was clearly separated from all other mormoopids—by a distance coefficient of 1.800 (Fig. 12B). Both ghost-faced bats, *Mormoops megalophylla* and *M. blainvillii,* were associated and set apart from other species by a distance coefficient of 1.470. However, the large naked-backed species, *suapurensis,* was set off from the smaller naked-backed species *davyi* by a distance coefficient of 1.140, the latter being aligned more closely with the species *personatus.* These two species do indeed resemble each other in size and, more or less, in the shape of the skull. The cophenetic correlation for this phenogram was 0.881, the influence of shape nearly balancing the effect of size. The per cent of trace along the *X* axis was 47.16, 39.41 on the *Y* axis, and 8.65 on the Z axis. The total effect of shape was to more or less balance the effect of size as seen in the relatively wider, higher projection (Fig. 13B). Although shape in conjunction with size gave a more reasonable arrangement than size alone, *suapurensis* and *parnellii* still seemed "out of place."

The next phase of the analysis was to quantify some of the more obvious qualitative characters. Following Sokal and Sneath (1963:77), I selected 20 characters from the cranial and external anatomy and coded these as non-additive multistate characters (see Methods). These characters represent an array of features that have, in the past, been weighed heavily (dorsal fusion of wing membrane), weighed lightly (shape of tragus and attachment of flight membranes to ankle), or not used at all (number of lobes on i2 and basining of nasal root). In accordance with procedures of numerical taxonomy, these characters were given equal weight as were the other 22 characters mentioned above and incorporated herein. The association of the two ghost-faced species was maintained with a distance coefficient of 1.680 from the remaining taxa (Fig. 12C). Again, *parnellii* is separated from the other taxa, but this time with a smaller distance coefficient (1.620). Both naked-backed species are allied and the two small Antillean species *macleayii* and *fuliginosus* retained their close association throughout the analysis; the greatest distance coefficient between these two insular taxa, 0.400, was observed in the first phase of the analysis (Fig.

12A). The species *personatus* still remains associated with *macleayii* and *fuliginosus* on the one hand as well as with *davyi* and *suapurensis* on the other; distance coefficients were 0.930 and 0.960, respectively. The cophenetic correlation for this phenogram was 0.938. The segregation of these taxa is more clearly illustrated in the projection (Fig. 13C). The majority of the trace is seen on the *X* and *Y* axis (47.59 and 32.71, respectively) with 9.29 on the *Z* axis. Although further analysis might affect the relative positions of the taxa, it is doubtful that drastic departures from the general arrangement presented above would occur. There remains the task of deriving a suitable classification from the above information.

At least three systematic interpretations of the results seem feasible. The least satisfactory of these choices would be to recognize four genera—*Phyllodia* (including the species *parnellii*), *Chilonycteris* (including *fuliginosus, macleayii,* and *personatus*), *Pteronotus* (including *davyi* and *suapurensis*), and *Mormoops* (including *blainvillii* and *megalophylla*). Such an arrangement would create a taxonomic imbalance, owing primarily to the great degree of difference between *Mormoops* and the other three genera. This classification (A1 in Fig. 14) would seem to require the adoption of two subfamilies, Chilonycterinae (including *Phyllodia, Chilonycteris,* and *Pteronotus*) and Mormoopinae *(Mormoops).* An advantage of this arrangement would be that it emphasizes the basic dichotomy within the family. However, recognition of subfamilies might tend to overemphasize the distinctness of *Mormoops,* and the allocation of the three apparent, but not unusually distinct, units *(Phyllodia, Chilonycteris, Pteronotus)* to generic rank would seem to oversplit the family at that level.

Another possible choice would be to recognize three genera (A2 of Fig. 14) —*Phyllodia* and *Mormoops* (with the included taxa described above) and *Pteronotus* (comprised of two subgenera *Chilonycteris* and *Pteronotus*). There probably would be no need for subfamilies in this arrangement and the recognition of subgenera within the genus *Pteronotus* would indicate the apparent close relationship between the two units included. However, the main dichotomy in the family would not be as conspicuous as in the previous classification, nor would it be readily apparent that *Phyllodia* is more closely allied with *Pteronotus* (as defined here) than to *Mormoops.*

As should be apparent now, there are two major problems to be considered in the formulation of a satisfactory

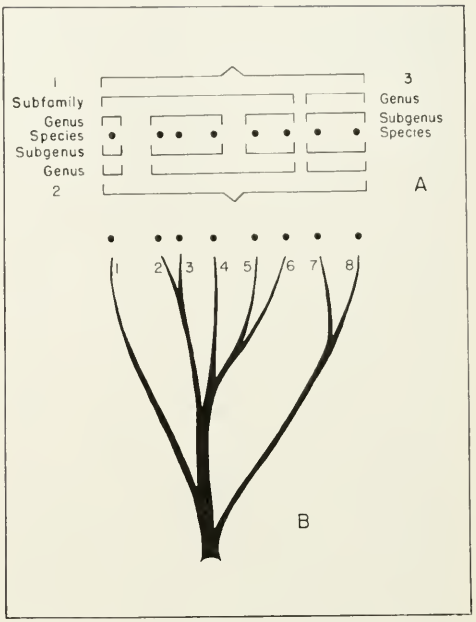


FIGURE 14. Possible systematic alternatives (A) to the supposed phylogenetic arrangement (B) of the mormoopid species: 1, *parnellii;* 2, *fuliginosus;* 3, *macleayii;* 4, *personatus;* 5, *davyi;* 6, *suapurensis;* 7, *blainvillii;* and 8, *megalophylla.* Each of three possible interpretations (discussed in text) can be deciphered by reading rows of brackets from left to right in estimations 1 and 2 and right to left in 3. The outermost bracket in each case signifies the familial level. The horizontal and vertical gaps in the "phylogenetic tree" (B) relate to degrees of inferred differences and similarities.

classification of the mormoopid bats. The first of these is the extreme distinctness of the bats of the genus *Mormoops*. These are easily distinguished on the basis of a number of characteristics (tragus, structure of humerus, lip and facial morphology, shape of cranium, size and shape of various teeth, for example) and there can be little doubt of their generic status. On the other hand, the bats that have been referred to as *Phyllodia, Chilonycteris,* and *Pteronotus* are not so distinct from each other as they are as a group from *Mormoops,* although *Phyllodia* does seem to be somewhat more distinct from *Pteronotus* and *Chilonycteris* than the latter two are from each other. These points, it seems to me, should be expressed, insofar as possible within the limitations of our current system of classification, in the interest of developing categories of more or less equal rank.

I propose the following classification (A3 in Fig. 14) as that which most closely represents the relationships within the Mormoopidae as now understood. Two genera, *Pteronotus* and *Mormoops,* are recognized and are assumed to be of approximately equal "taxonomic rank." This seems reasonable in view of the overall nature of variation in the family and the apparent basal dichotomy. The genus *Pteronotus* is the less specialized of the two. This is apparent, I think, in the rather generalized structure of the distal end of the humerus (Fig. 4, A-D) and generalized to moderately specialized tragus (Fig. 10, A-F), and by the lesser degree of development of lip and facial excrescences and the long, pointed ears that are not connected (or only slightly so) over the nose. The genus *Mormoops,* on the other hand, appears to be much more specialized in these features. The crania of these two genera are markedly different, especially because of the curious flexion in *Mormoops,* which may be related to orientation of the mouth to an extreme anterior position where it can act more efficiently as a scoop for insects during foraging. Inflation of the braincase in the postparietal regions may reflect major specializations of the posterior portion of the brain that in turn relate to more integrated control of certain neural activities.

I have chosen to divide the genus *Pteronotus* into three subgeneric units—*Phyllodia, Chilonycteris, Pteronotus*—to indicate the existence of at least three distinct, yet closely related, lines of development. The subgenus *Phyllodia* seems to be the most generalized and is set off from *Chilonycteris* and *Pteronotus* as indicated by the slightly larger distance coefficient 1.680 (Fig. 12C). In addition to the above considerations, this classification is the most conservative and, as such, is probably the best suited at this stage of our knowledge of chiropteran systematics.

Patterns of Non-geographic Variation

In order to assess the patterns of geographic variation within individual species of the Mormoopidae, it was first necessary to examine several features of the non-geographic variation—namely secondary sexual variation, individual variation, and seasonal variation with reference to pelage and molt. I have not been particularly concerned in this study with variation with age because mormoopids appear to mature rather rapidly, and once coalescence of epiphyseal and cranial sutures has occurred it is relatively difficult to distinguish young adults from older animals. For the purposes of this study, specimens that had completely fused phalageal epiphyses and cranial sutures and a fully erupted dental arcade were judged as adults.

Secondary sexual variation.—At the outset of this study, I examined representative populations of *Pteronotus personatus, P. davyi,* and *Mormoops megalophylla* in order to determine whether it would be necessary to segregate the sexes during the initial data collection;

significant secondary sexual variation was apparent. Results of subsequent tests on several relatively large samples of *Pteronotus parnellii, P. personatus, P. davyi,* and *Mormoops megalophylla* revealed some interesting aspects of mormoopid secondary sexual variation (Fig. 15). With several exceptions, probably due to sample size, males were as large as, or larger than, females of the same species from the same geographic area. The kind and degree of secondary sexual variation differed locally; that is, the sexes of a species were not always significantly different in the populations tested. In cases when samples were significantly different, they did not necessarily vary in the same characters from one population to the next. For example, males and females of *P. parnellii* (Fig. 15) from Sinaloa, México, differed significantly in a single character, the zygomatic breadth. Males and females from Jalisco differed by two characters —zygomatic breadth and condylobasal length. In a population of *parnellii* from Amazonas, Venezuela, the sexes differed significantly by every character except length of the forearm and breadth of the interorbital constriction. No single character was observed to vary consistently throughout all samples of *parnellii* tested, although condylobasal length and depth of the cranium were significantly different between males and females from nearly every locality tested.

In *P. personatus,* the breadth across the mastoid flanges and depth of the cranium were consistently different in each sample tested (Fig. 15). However, heterogenous secondary sexual variation was also observed in this species. Of the four species tested, *Mormoops megalophylla* exhibited the least amount of secondary sexual variation within the populations tested.

In both *P. parnellii* and *personatus* distance coefficients between sexes become progressively larger southwardly in the range of the species. This general trend is most striking in populations of *parnellii.* The one insular population (from Jamaica) of this species also exhibits considerable distinctness between males and females. On the other hand, *P. davyi* seems to show a reverse trend with the greatest difference between males and females observed in the most northerly (Sonoran) population (Fig. 15), although the Guatemalan sample also shows a relatively high distance coefficient. Testing of more southerly populations of *personatus* and *davyi* was unsatisfactory owing to small samples.

Generally, the males and females of *Mormoops megalophylla,* although differing in several characters, exhibited consistently lower distance coefficients than other mainland species analyzed. No readily apparent geographic trend in secondary sexual variation was detected, and much of the variation observed appears to be random.

The endemic Antillean species *Pteronotus fuliginosus, P. macleayii,* and *Mormoops blainvillii* could not be satisfactorily tested due to insufficient sample sizes. Zygomatic breadth, breadth of the braincase, and breadth of the postpalatal extension were slightly different in the Cuban population of *P. macleayii.* Males and females of *P. fuliginosus* from Puerto Rico exhibited marked differences in mastoid breadth, breadth of rostrum, length of maxillary and mandibular toothrows, and depth of cranium. Other smaller differences were recorded in length of the forearm and zygomatic breadth. The small *Mormoops blainvillii* from Puerto Rico, like the mainland *M. megalophylla,* showed only slight secondary sexual differences.

Only a preliminary and highly speculative interpretation of the meaning of the observed secondary sexual variation in mormoopids can be made. Little is known about the ecology and interspecific interaction of the majority of Neotropical bats, to say nothing of interaction between sexes of one species.

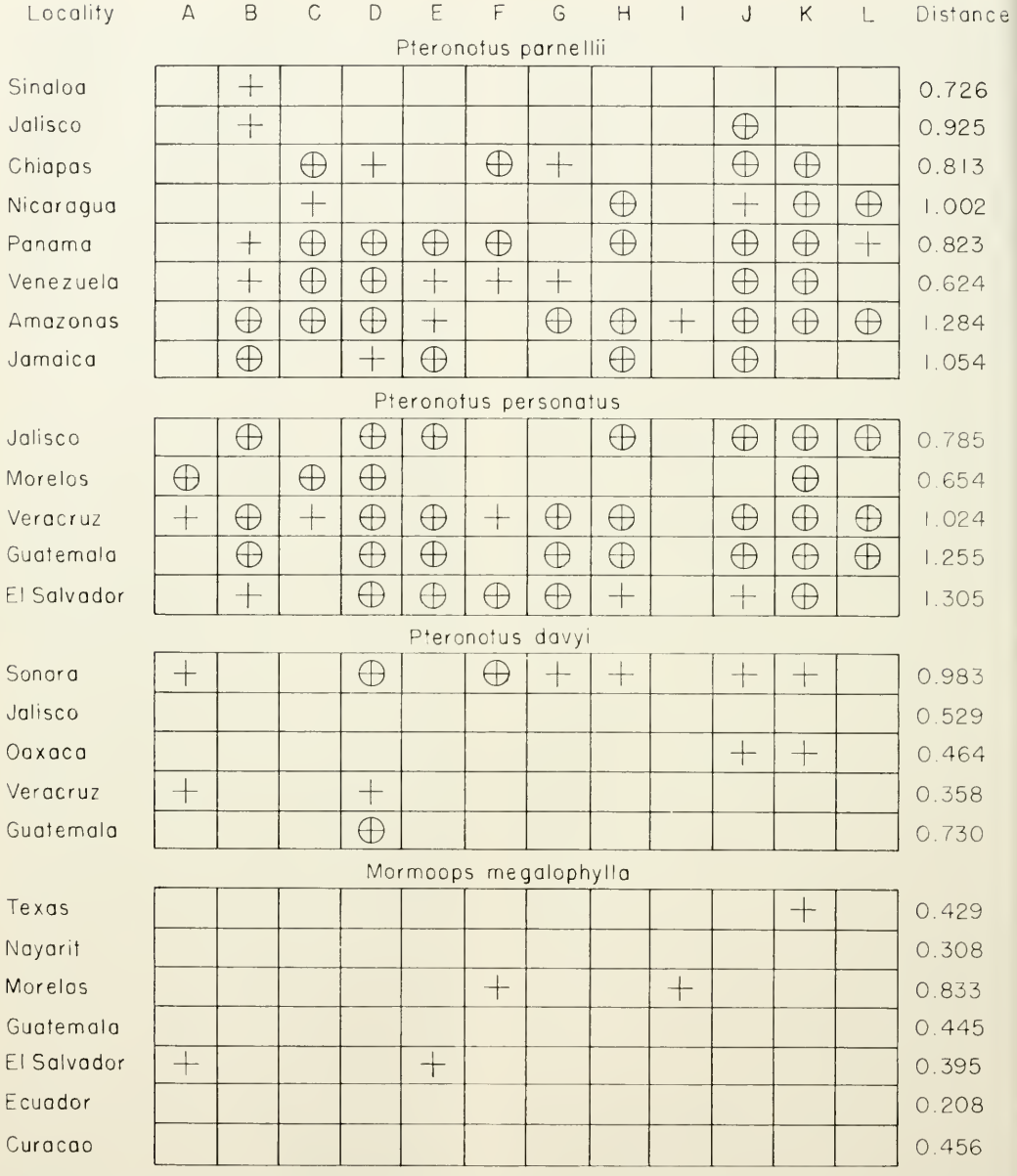


FIGURE 15. Secondary sexual variation in 12 external and cranial dimensions (A-L) of four mormoopid bats. Dimensions are as follows: A, length of forearm; B, zygomatic breadth; C, breadth of braincase; D, mastoid breadth; E, zygorostral length; F, interorbital breadth; G, rostral breadth; H, length of maxillary toothrow; I, breadth of post-palatal extension; J, condylobasal length; K, depth of braincase; L, length of mandibular toothrow. A plus indicates that the character was significant at the 0.05 level of probability, whereas a plus and circle indicate significance at the 0.01 level. Coefficients of distance between the larger males and females appear in the far right-hand column for each locality. See text for discussion.

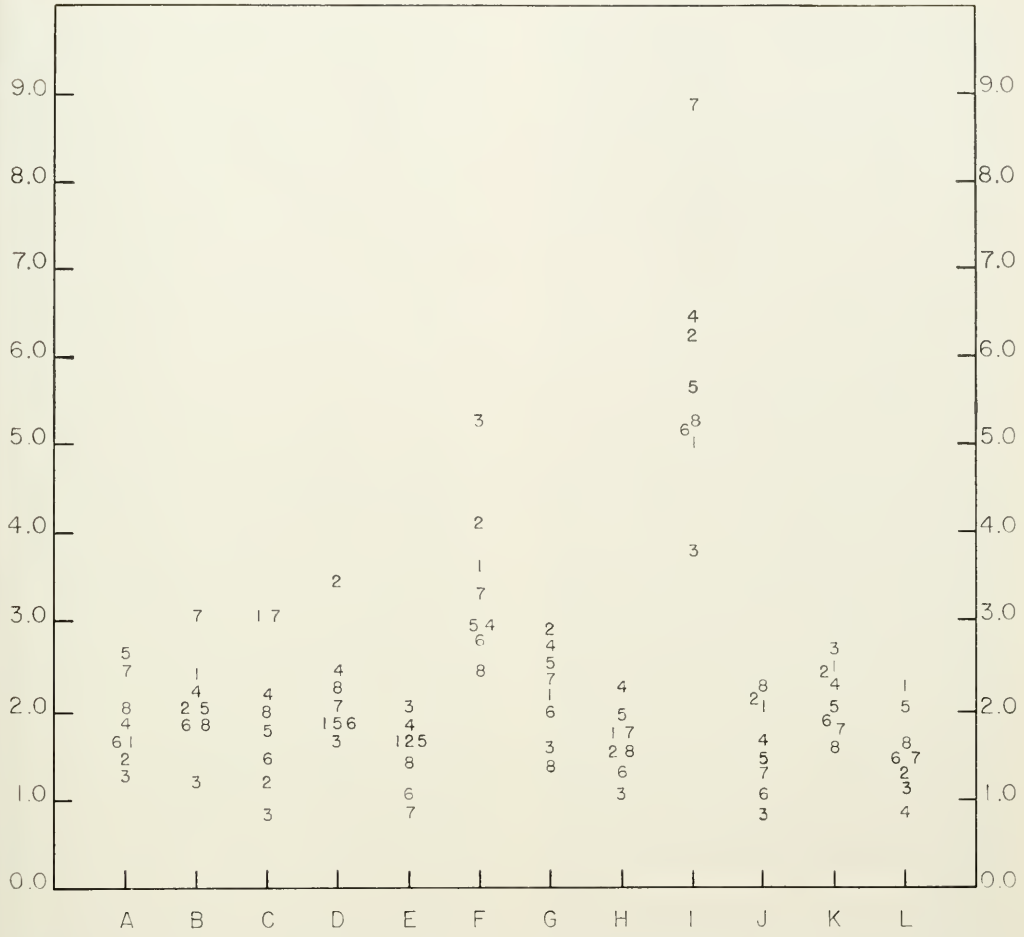


FIGURE 16. Coefficients of variation (ordinate) of external and cranial dimensions used in this study. These dimensions (abscissa) are as follows: A, length of forearm; B, zygomatic breadth; C, breadth of braincase; D, mastoid breadth; E, zygorostral length; F, interorbital breadth; G, rostral breadth; H, length of maxillary toothrow; I, breadth of post-palatal extension; J, condylobasal length; K, depth of braincase; and L, length of mandibular toothrow. The plotted numbers refer to mormoopid taxa as follows: 1, *Pteronotus fuliginosus;* 2, *P. macleayii;* 3, *parnellii;* 4, *P. personatus;* 5, *P. davyi;* 6, *P. suapurensis;* 7, *Mormoops blainvillii;* 8, *M. megalophylla.*

Perhaps males are utilizing the "niche" in different ways than are females, which could conceivably account for differences in size. An interpretation of the geographic trends in sexual distinctness is even more difficult. In the case of Sonoran *P. davyi,* the less than optimal xeric habitat might cause direct competition between sexes of equal size, whereas in more favorable mesic habitats there is less emphasis on competition between males and females. This interpretation, however, does not seem to fit the situation found in either *P. parnellii* or *P. personatus.* Nevertheless, the observed differences seem to represent real variation and certainly merit further investigation.

Individual variation.—Most characters examined in this study revealed relatively little individual variation in all species; coefficients of variation for characters usually were low (Fig. 16). The breadth across the post-palatal ex-

tension was the most variable parameter tested; coefficients of variation in this measurement ranged as high as 5.0 to approximately 9.0. Generally, individual values were tightly clustered around the mean, giving a bell-shaped, normally distributed curve that in most cases was tall and narrow with a relatively wide base; the curve frequently was skewed.

Externally, a small amount of individual variation was observed. Several species, *Pteronotus personatus, macleayii,* and *fuliginosus,* have two to four tooth-like serrations on the proximal edge of the pinna. The number of rows of wart-like bumps on the central pad of the lower lip also varied intraspecifically. No marked variation was observed in the structure of the tragus. The wing membrane of mormoopid bats usually is black, whereas many other Neotropical bats (especially phyllostomatids) commonly have a white (nonpigmented) blotch extending from about the middle of the second phalanx of the third digit to the wing tip. Only one individual of a mormoopid (USNM 370057, *Pteronotus parnellii,* from Rancho Grande, Venezuela) possessed white wing tips.

Phillips and Jones (1969:516-520) reported no dental abnormalities in specimens of *Pteronotus fuliginosus, macleayii, suapurensis,* or *Mormoops blainvillii.* Several individuals of *P. parnellii, personatus, davyi,* and *M. megalophylla* had lost one or more teeth in life, and a few cases of developmental anomalies were found. I examined one specimen of *P. fuliginosus* (ROM 37128) from St. Clair Cave, Jamaica, with an extra left upper incisor; the anomalous tooth was slightly smaller than I2 and was squeezed between it and the canine. A disease-caused anomaly was observed in a specimen of *Mormoops megalophylla* (UMMZ 109750) from near San Cristóbal, Chiapas, in which the entire protocone and hypoconal shelf was eroded away on both first upper molars. The erosion was almost perfectly symmetrical on both of these teeth; only the W-shaped cusp pattern remained. Carlton J. Phillips (personal communication) indicated that this condition might have been caused by *dentinogenesis imperfecta,* which results in a breakdown and rapid erosion of the dentine layer of the tooth.

Pelage and molt.—Past workers thought two distinct "color phases" occurred in mormoopid bats. Quite frequently, reddish or orangish bats and brownish bats were found in collections near or at the same locality and taken at the same time of year. In fact, Thomas (1892a) based the name *Pteronotus davyi fulvus* on a brightly-colored (fulvous) individual. Also, Wagner's (1843) specific name *rubiginosa* suggests the reddish color of his Brazilian specimen; J. A. Allen (1911) applied the subspecific name *fusca* to fuscous brown specimens of *P. parnellii* from northwestern Venezuela. Allen (1894) also discussed color phases of *P. davyi* and concluded that these were of no particular value in judging subspecific differences. At the outset of my study, it seemed reasonable to suspect genetic polymorphism in color among mormoopids. Peculiarities of the molt process in this group, coupled with the paucity of molting individuals in collections, may explain why it did not occur to previous investigators that "color phases" might be related to some biochemical change due to aging of the hair or bleaching from environmental sources (ammonia concentration from guano, for example), or a combination of both.

In the summers of 1966 and 1967 in Nicaragua, several individuals of *Pteronotus parnellii* were captured that had a brilliant fulvous band around the outer margins of the haired portion of the body, including a narrow ring around the base of the ears, the anal-genital region of one female, and on the tip of the nose. The remaining areas of the body had a dark brown, glossy pelage. Except for slight discoloration on

the skin of the upper flanks, there was no sign of active molt. Upon microscopic examination of the pelage of these specimens I found individual reddish hairs interspersed among the new brown hairs. The density of reddish hairs decreased near the midline, whereas brownish hairs, although present, were infrequent in the lateral reddish band. Further investigation revealed that the so-called "color phases" are entirely related to changes in color associated with the annual molt.

The progression of molt and changes in color of hair are discussed below for *Pteronotus parnellii*. All other mormoopids follow this same general scheme, with a few modifications that are mentioned in the discussion. Fresh pelage in *parnellii* usually is dark Prout's Brown to blackish, depending somewhat on geography. As the pelage ages, it becomes gradually paler (Snuff Brown). Exactly what causes this change is not presently understood, although several workers (Constantine, 1958a, 1958b, and Mitchell, 1964) have related bleaching of hair to ammonia, which accumulates in high concentrations in guano-filled caves. At any rate, the change in color may progress all the way to a brilliant fulvous or orange. In the latter case, new molt is obvious.

Generally, molt begins on the nape and throat with extensive loss of hairs. As hair is replaced in these areas, several centers (usually symmetrically located) of discoloration of the skin, and possibly new hair growth, can be detected slightly anterior to (or between) the ears, in the shoulder region over the scapulae, and in a single middorsal patch on the rump (Fig. 17). Ventrally, there appears to be only a single center —the throat region (Fig. 17)—from which active hair replacement progresses. These centers continue to expand in all directions (Fig. 17) until a single continuous band of active hair replacement encircles the body. Molt seems to progress more rapidly on the dorsum than on the venter and continues until new hair is apparent over the entire surface of the body. In many cases, significant molt progression takes place before it is readily noticeable. At stage 4 or 5 (Fig. 17), the old pelage begins to slough off in patches or by individual hairs. Active molt may terminate and the skin return to normal coloration before portions of the old pelage are sloughed at the peripheral edges of the haired surfaces (as described above for the Nicaraguan material). Eventually, all of the old fulvous hairs fall out leaving the darker fresh pelage.

Apparently, the rate at which the hairs change color varies individually and may be a phenotypic expression of some genetically caused differences in biochemical composition of the hair. Environmental factors such as ammonia concentrations may amplify this color change. Another factor that seems to be important is the reproductive cycle, which may delay molt in pregnant or lactating females and thereby allow for continued color change in old pelage.

There seems to be but one molt annually in mormoopid bats; most populations of *Pteronotus* molt from May to July, whereas molt in *Moormoops megalophylla* occurs from June to September. Because of a paucity of material, I am uncertain if mormoopids undergo a second molt, but several molting individuals (usually females that were apparently in terminal lactation) were collected in October, November, December, and early January. Nevertheless, most individuals of *Pteronotus* are ready to molt near the onset of the rainy season, the time at which *Pteronotus* are reproducing. Since both processes are seemingly stressful physiological conditions, it is not unreasonable to presume that only one occurs at any given time. Therefore, one might suspect that in May and early June the males, freed from their less strenuous reproductive cycle, are beginning to molt. Males and non-pregnant, non-lactating females

FIGURE 17. Generalized diagram of molt progresssion in mormoopid bats. This sequence (based on *Pteronotus parnellii*) and deviations from it are discussed in text. The top (dorsal views) and bottom (ventral views) rows depict molt progression (stages 1-6) from left to right.

molt mostly within this period, and both sexes have fresh pelage in July and August. On the other hand, reproducing females, judged by the presence of embryos or enlarged, discolored mammae (a presumed indication of lactation) were found throughout April, May, June, and early July with increasingly redder pelage. Probably shortly after termination of lactation, these females molt from the brilliant fulvous pelage to the darker fresh pelage. Occasionally, males with old fulvous pelage and no apparent molt in progress were found in August.

All of the bats of the genus *Pteronotus* follow the general molt pattern outlined above. In the subgenus *Chilonycteris*, where the fresh pelage consists of white or grayish hairs interspersed among the darker hairs, the terminal phases of molt (stages 4 and 5, Fig. 17) may result in a beautifully-colored individual tinged with orange, gray, and white. Progression of the molt in the naked-backed *P. davyi* and *P. suapurensis* is similar to that in *P. parnellii*, at least that part of the molt that can be seen readily; events that occur under the fused wing membrane are not known.

Constantine (1958a) reported on color variation and molt in *Mormoops megalophylla* from Frio Cave, Texas. The molt progression described by him is similar to that of *P. parnellii* shown in figure 17. However, there are several noteworthy differences in the character of the pelage of these two mormoopid genera. Whereas the hairs of *Pteronotus* are short, stiff, and usually monocolored (bicolored in the Antillean species), those of *Mormoops* are long, lax, and have at least four distinct color bands. The basal band occupies about one-fifth of the filament length and is dark

brownish (Prout's Brown). This basal band changes color abruptly to a paler whitish or pinkish buff band that is two or two and one-half times as wide as the basal band. The third color band is about equal in length to the basal band, is buffy brown, and not sharply delineated from the preceding band. The hair filament is tipped with a dark brownish band. Constantine (1958a: 345) described a fifth color band ("zone X") that he found irregularly between bands two and three, but the color gradation between these two bands is so gradual that I was unable to detect this fifth zone of coloration with any regularity.

Although "color phases" do exist in the genus *Mormoops*, they are not so distinct nor so striking as those in *Pteronotus*. As the pelage of *Mormoops megalophylla* ages, the wide second color band gradually becomes redder; eventually the entire filament may be affected. The presence of several other color bands may contribute to the subtle change in the color of the hair. In any event, once the reddish tinge has been incorporated into the middle paler bands the overall appearance of the pelage becomes reddish. This I suspect is the explanation for the reddish colored *M. megalophylla* from western México, named as a distinct subspecies by Davis and Carter (1962:65). None of the material examined, including the holotype and type series of these bats (collected on 26 July), was in what might be called "fresh pelage." In fact, there are three adult males (KU 94032, 94034, and 94035) from near Santa Lucía, Sinaloa, collected on 28 July, that are in the process of molting from the "characteristic" reddish or rufus pelage to a darker, more grayish pelage. Nothing is known concerning the molt sequence of *M. blainvillii*, but I presume it resembles that described above for *M. megalophylla*.

Key to the Genera and Subgenera

1. Rostral portion of cranium elevated, producing abruptly rising forehead; p2 not noticeably reduced in size (as compared with p1); tragus complex, with extensive secondary fold (Fig. 10); ears funnel-shaped and round, lacking a long lanceolate portion, and united on the rostrum by a pronounced band ... Genus *Mormoops*

   Rostral portion of cranium not or only slightly elevated, braincase and rostrum more or less in same plane; p2 reduced in size to a small, peg-like, unicuspid tooth; tragus with secondary fold small to moderately large (Fig. 10); ears funnel-shaped, with pronounced lanceolate portion, noticeably separated but may be connected by a low, inconspicuous ridge ... Genus *Pteronotus*

2. Wing membrane fused on middorsal line giving a naked-backed appearance; rostral breadth always greater than length of maxillary toothrow ... Subgenus *Pteronotus*

   Wing membrane not fused on middorsal line; rostral breadth equal to or less than length of maxillary toothrow ... 3

3. Basioccipital narrowly constricted between auditory bullae; basisphenoid with two narrow and deep furrows; forearm usually more than 50 mm ... Subgenus *Phyllodia*

   Basioccipital not constricted between auditory bullae; furrows in basisphenoid wide and shallow; forearm usually less than 50 mm ... Subgenus *Chilonycteris*

Genus **Pteronotus** Gray

Mustached and Naked-backed Bats

Pteronotus Gray, 1838, Mag. Zool. Bot., 2:500, February.

Chilonycteris Gray, 1839, Ann. Nat. Hist., 4:4, September (type, *Chilonycteris macleayii* Gray). Valid as a subgenus.

Lobostoma Gundlach, 1840, Arch. Naturgesch., 4:357 (type presumably *Lobostoma quad-*

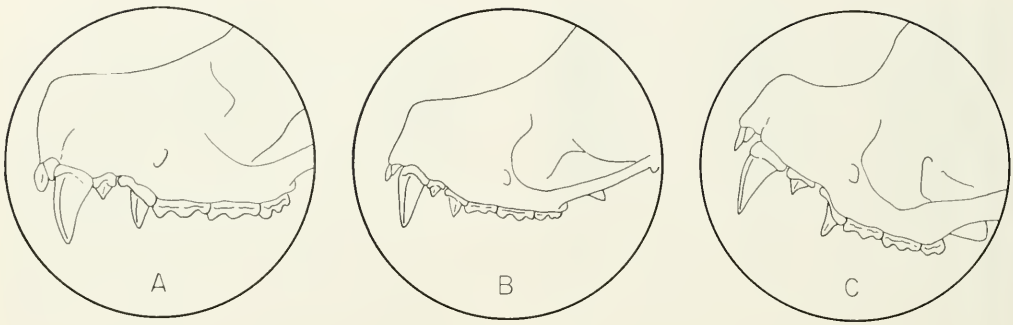


FIGURE 18. Side view of rostral portion of crania of three mormoopids showing maxillary root of zygomatic arch and position of infraorbital foramen. A, *Pteronotus parnellii;* B, *Pteronotus personatus;* and C, *Mormoops megalophylla.* Horizontal line below B is 5 mm in length.

ridens Gundlach = *Chilonycteris macleayii* Gray).

Phyllodia Gray, 1843, Proc. Zool. Soc. London, p. 50, October (type, *Phyllodia parnellii* Gray). Valid as a subgenus.

Dermonotus Gill, 1901, Proc. Biol. Soc. Washington, 14:177, September 25. Replacement name for *Pteronotus* Gray, 1838, thought to be preoccupied by *Pteronotus* Rafinesque, 1815, a *nomen nudum* (see Miller, G. S., Jr., Proc. Biol. Soc. Washington, 18:223, 17 October 1905).

Type species. — *Pteronotus davyi* Gray, 1838.

Distribution.—Humid to semixeric Neotropics (generally below 3000 meters) from southern Sonora and Tamaulipas, México (excluding Baja California and portions of the Mexican plateau), southward through British Honduras, Central and South America (including Trinidad) to the Mato Grosso region of Brasil (excluding Dutch West Indies). Two endemic species, *fuliginosus* and *macleayii,* and several subspecies of *parnellii* are found in the Greater Antilles. *Pteronotus davyi* is also found on the leeward Antillean islands of Grenada, Dominica, Marie Galante (off Guadaloupe), and Martinique. For further information regarding distribution, see the following species accounts.

Description.—Bats of this genus are highly variable in size. *Pteronotus fuliginosus torrei* from Cuba is the smallest representative of the family, and *Pteronotus parnellii rubiginosus* from South America and *Pteronotus suapurensis* from Central America are among the largest members of the family. Externally, members of this genus are easily distinguished from the genus *Mormoops* by short, stiff pelage, long pointed pinnae of ears that may be weakly connected dorsally by a low ridge on the rostrum that is confluent with a small V-shaped rostral tubercle, proximal portion of the pinna funnel-shaped and confluent at lower edge with lower lip, plagiopatagium and uropatagium firmly attached directly to ankle or to tibia by a tightly bound ligament, tragus lanceolate with a small secondary fold on cranial edge or spatulate with a marked secondary fold (Fig. 10, A-F).

The cranium is "normal" in appearance; that is, the rostrum and braincase are, more or less, in the same plane. The rostrum may be slightly tipped upward in the subgenus *Pteronotus,* but never is so extremely elevated as in *Mormoops.* The zygomatic arches are complete and well developed, and lie, more or less, in the same horizontal plane as the rostrum and braincase. The lambdoidal ridges are strongly developed and form a prominent flange from the posteriormost part of the low sagittal crest to the tip of the short mastoid process that overlays the tym-

panic bulla posterior to the external auditory meatus. Viewed from the ventral side, the presphenoid, which lies between the pterygoid wings and forms the roof of the mesopterygoid fossa, is elevated "above" the level of the basisphenoid giving it a "step" appearance. In all species except *P. personatus*, the infraorbital foramen opens (on the side of the rostrum at about its widest point) at the end of a short, tubular canal that is visible through the thin bone of the maxillary. In *P. personatus* and in *Mormoops* this foramen opens abruptly at the anterior root of the zygomatic arch, the canal being formed only by a thin, bridge-like spicule of bone (Fig. 18).

The molars are typically dilambdodont, and the entire dental arcade is compact, without striking diastemas. The upper incisors are prominent and fill the space between the canines. The lower incisors are generally trifid, small, and bear a lingual heel. In the subgenus *Phyllodia*, these teeth are large and bulky. The second lower premolar is markedly reduced to a small peg-like, unicuspid tooth and is almost always excluded (lingually), or nearly so, from the toothrow.

Subgenus **Phyllodia** Gray

Type species.—*Phyllodia parnellii* Gray, 1843.

Geographic distribution.—Greater Antilles and on the mainland from southern Sonora and Tamaulipas, México, southward along Pacific and Gulf coastal lowlands, throughout Central America, and into South America where it occurs along the Caribbean coast (including Trinidad) and south into the Amazon Basin to the Mato Grosso region of Brasil. These bats have not been reported from west of the Andes in Colombia, Ecuador, or Perú, nor from French Guiana or eastern Brasil.

Description.—Size medium to large; wing membranes attached low on sides of body and attached to ankles by way of a short, tightly bound ligament; back covered by a wide band of short stiff hairs; labio-nasal plate simple; margin above each nostril with several irregular, wart-like tubercles; deep emargination between nostrils; area lateral to nostrils lacking spike-like projection (Fig. 11A); tragus simple, lanceolate, secondary fold small (Fig. 10A); antero-medial edge of ear pinnae smooth, lanceolate portion broad; ears connected by two low, inconspicuous ridges that fuse on top of the muzzle forming a prominent rostral tubercle; profile of skull relatively flat, rostrum not elevated, forehead sloping gradually onto rather long, broad braincase; upper incisors robust and peg-like, inner pair distinctly bifurcate and with broad, rounded heel; lower incisors also heavily constructed, inner pair trilobed, outer pair bilobed; tympanic rings small in proportion to those of other subgenera, covering approximately one-third of the auditory bullae; basioccipital region narrowly constricted between bullae and with two narrow and deep longitudinal furrows into which the *M. longus capitis* inserts.

Remarks.—This monotypic subgenus is quite distinct and is not liable to be confused with either of the other subgenera—*Chilonycteris* or *Pteronotus*. Novick (1963a:47) noted that the acoustic orienting pulses emitted by *P. parnellii* were strikingly different from those of any other mormoopid or phyllostomatid studied by him.

Pteronotus parnellii (Gray)
PARNELL'S MUSTACHED BAT

(Synonymy under subspecies)

Distribution.—Same as for subgenus (Fig. 19).

Description.—See account of subgenus.

Relationships.—In many respects, *Pteronotus parnellii* is the most primitive member of the family Mormoopidae. The tragus is not so ornamented as in other species of the family, which tend toward complexity through empha-

59	21.50	I
58	21.35	II
54	21.25	II
57	21.24	III
41	21.12	III
37	21.09	IIII
60	20.99	IIIII
40	20.96	IIIIII
43	20.92	IIIIIII
35	20.88	IIIIIIII
55	20.87	IIIIIIIII
31	20.85	IIIIIIIII
53	20.81	IIIIIIIIII
42	20.80	IIIIIIIIIII
45	20.79	IIIIIIIIIII
56	20.73	IIIIIIIIIIII
44	20.62	IIIIIIIIIIII
36	20.57	IIIIIIIIIIII
38	20.55	IIIIIIIIIII
47	20.54	IIIIIIIIIII
39	20.48	IIIIIIIIII
51	20.48	IIIIIIIIII
46	20.39	IIIIIIIIII
50	20.38	IIIIIIIII
34	20.35	IIIIIIIII
33	20.34	IIIIIIIII
28	20.32	IIIIIIIII
27	20.31	IIIIIIIII
49	20.31	IIIIIIII
48	20.30	IIIIIIIII
14	20.29	IIIIIIII
30	20.28	IIIIIIII
52	20.26	IIIIIIIII
25	20.23	IIIIIIII
26	20.22	IIIIIIII
32	20.21	IIIIIIII
13	20.17	IIIIIIII
29	20.13	IIIIIIIII
22	20.10	IIIIIIIIII
20	20.07	IIIIIIIII
17	19.90	IIIIIIIIII
24	19.89	IIIIIIIII
23	19.82	IIIIIIIIII
16	19.77	IIIIIIIIII
15	19.70	IIIIIIIII
21	19.67	IIIIIIIIII
11	19.62	IIIIIIIII
12	19.55	IIIIIIII
7	19.50	IIIIIII
5	19.48	IIIIIII
8	19.44	IIIIII
4	19.42	IIIIII
9	19.41	IIIIII
10	19.39	IIIII
6	19.34	IIII
62	19.21	IIII
18	19.18	IIII
19	19.17	III
2	19.15	III
3	19.13	III
61	19.12	II
65	18.90	I
1	18.90	I
63	17.47	I
64	16.40	I

A

58	13.11	I
59	13.06	II
60	13.05	III
54	13.01	IIII
57	12.98	IIIII
41	12.97	IIIII
37	12.91	IIIIII
55	12.90	IIIIIII
35	12.87	IIIIIIII
43	12.85	IIIIIIII
36	12.80	IIIIIIIII
44	12.80	IIIIIIIII
42	12.79	IIIIIIIII
56	12.77	IIIIIIIIII
38	12.75	IIIIIIIIII
53	12.71	IIIIIIIIIII
40	12.68	IIIIIIIIIII
45	12.67	IIIIIIIIIII
34	12.65	IIIIIIIIIII
31	12.61	IIIIIIIIIII
30	12.58	IIIIIIIIIII
39	12.55	IIIIIIIIIII
51	12.53	IIIIIIIIIII
46	12.51	IIIIIIIIII
22	12.50	IIIIIIIIIII
32	12.46	IIIIIIIIII
27	12.44	IIIIIIIII
48	12.42	IIIIIIIIII
50	12.42	IIIIIIIII
14	12.40	IIIIIIIII
29	12.39	IIIIIIII
28	12.38	IIIIIIII
25	12.37	IIIIIII
47	12.36	IIIIIIII
20	12.35	IIIIIIII
33	12.34	IIIIIII
13	12.31	IIIIIIII
26	12.30	IIIIIIIII
49	12.28	IIIIIIIII
17	12.23	IIIIIIIIII
16	12.16	IIIIIIIIII
15	12.16	IIIIIIIIII
24	12.07	IIIIIIIIII
52	12.06	IIIIIIIIII
23	12.03	IIIIIIIIII
21	11.97	IIIIIIIII
9	11.91	IIIIIIII
18	11.90	IIIIIII
12	11.87	IIIIIII
11	11.85	IIIIIII
7	11.84	IIIIII
8	11.81	IIIII
5	11.79	IIII
19	11.78	IIII
6	11.73	IIII
4	11.72	IIIII
10	11.71	IIIIII
3	11.58	IIIII
1	11.57	IIII
2	11.55	III
62	11.34	III
61	11.13	III
65	11.02	III
63	10.25	II
64	10.15	I

B

FIGURE 19. Results of two typical SS-STP analyses (A, condylobasal length and B, zygomatic breadth) of geographic variation of *Pteronotus parnellii*. Vertical line to the right of each array of means connect maximally non-significant subsets at the 0.05 level; for example, locality 59 with a mean condylobasal length of 21.50 is not significantly different from localities 58-56 with means ranging from 21.35 to 20.73, but does differ significantly from all other localities. See text for key to localities.

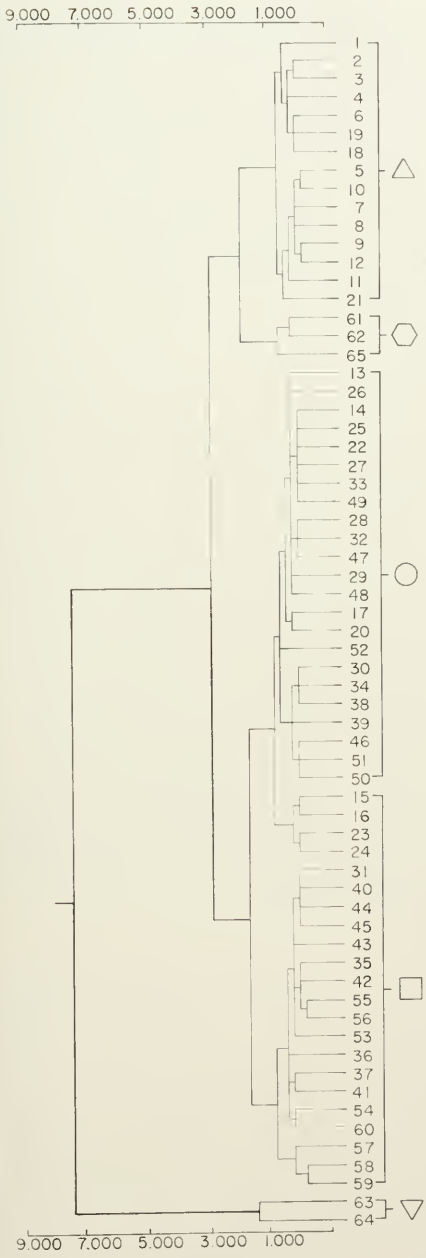


FIGURE 20. Phenogram of geographic variation of *Pteronotus parnellii* computed from the distance matrix on standardized locality means and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation for this phenogram is 0.863. Symbols to the right of the phenogram relate to localities as plotted in figure 21. See text for key to localities.

sis of a secondary fold (Fig. 10). Secondly, the rostrum is only slightly elevated and maintains an "in line" position with the braincase, whereas the upturned snout in other mormoopid bats seems to be an adaptation for more efficient feeding and/or echolocation. The braincase is large and bulky and may reflect a generalized brain with less refined control centers than in other species, and the extra long sonic pulses (as reported by Novick, 1963a) emitted by this species may indicate a more generalized mode of echolocation. On the basis of close resemblance *P. parnellii* seems to have its closest ties with the subgenus *Chilonycteris* and particularly with the species *P. personatus*. Apparently *P. parnellii* diverged from the mainline of mormoopid evolution at a rather early time.

Geographic variation.—As previously understood, *parnellii* was divided into eight geographic races—three on the mainland and five on the Greater Antilles (one of which, *P. p. gonavensis*, is known only from sub-Recent cave deposits). Prior to Koopman's (1955) report, the insular and mainland populations were regarded as distinct species, *parnellii* and *rubiginosus*, respectively. Koopman's proposition that they were conspecific has caused some controversy, not particularly concerning the relationships of the bats, but with the name to be used if the two groups are conspecific. This problem, which concerns date of publication and priority, has been discussed by de la Torre (1955: 696), Felten (1956:72), Koopman and Martin (1959:4-5), Husson (1962:75-76), and recently by Jones (1966:448). The International Code (Article 21b, ii, p. 19) is explicit about interpreting the date of publication when the exact date of issue within a year is unknown, as in the case of *rubiginosus* Wagner, 1843. This work must be considered as having been published on the last day of the year, 31 December 1843, thereby giving priority to Gray's name, *parnellii*, which

was published in October of that year. Furthermore, de la Torre's argument (1955:696) that *rubiginosus* should be retained because it is "the better known and more widely used name" has no basis because the name *parnellii* has been consistently used in the primary literature dealing with Antillean bats.

Although the above considerations are important, the basic concern is whether or not these two taxa are members of the same biological species. Because it is doubtful that direct evidence of intergradation between Antillean and mainland populations ever will be available, conspecificity can be judged only on the basis of resemblance. All of the insular populations are smaller in cranial and external size than are those from the mainland (Table 1), although *P. p. parnellii* from Jamaica is only slightly smaller than *P. p. mexicanus* from western México. The pelage of the Antillean races of *parnellii* appears to be "tricolored" dorsally, owing mostly to a more pronounced whitish central zone on the hair filaments in contrast to the darker basal and terminal zones. These zones of color on the hairs of the back cannot be called color bands because there is a gradual change from one to the other, in contrast to an abrupt, sharply defined change of color as seen on hairs of the venter. Insular populations average slightly paler in color than most mainland subspecies. The tragus of the insular bats closely resembles that of mainland specimens except that the distal half is slightly broader. In other respects, there is little difference between insular and mainland bats and at this time there seems to be nothing to gain by splitting these at the specific level.

In two typical results of the SS-STP analyses (Fig. 19) sample means of the Antillean populations (localities 61-65) are located at the small extreme of the size variation. It is also apparent that there are two groups within these insular populations. One of these includes larger bats from Cuba, Jamaica, and Puerto Rico (localities 61, 62, and 65, respectively), and the other contains smaller individuals from Hispaniola and La Gonave (localities 63 and 64). These two groups are separated by a distance coefficient of 7.800 in the distance phenogram (Fig. 20). In this phenogram, the grouping together of localities 63 and 64, which correspond to *P. p. pusillus* and *P. p. gonavensis*, respectively, indicates their similarity and their rather marked distinctness from other populations of *P. parnellii*. However, the distance coefficient of 1.800 between locality 63 and 64 also indicates a notable degree of distinctness between *pusillus* and *gonavensis*.

In the couplet encompassing localities 61, 62, and 65, Cuba and Jamaica (61 and 62) are more closely associated than either is to Puerto Rico (65), suggesting a close relationship between specimens from Cuba and Jamaica. On the other hand, the geographic position of Puerto Rico and the distinctness of the interposed populations of Hispaniola and La Gonave suggest independent variation of the Puerto Rican bats. These features are discussed in greater detail in the subspecies accounts that follow.

The mainland populations of *P. parnellii* are currently assigned to three geographic races: *mexicanus* Miller (1902:401) from southern Sonora and Tamaulipas south to the region of the Isthmus of Tehuantepec in southern México; *fuscus* J. A. Allen (1911:262) from southern México through Central America to the Caribbean coast of northern Colombia and Venezuela (individuals from Trinidad were assigned to this race by Goodwin and Greenhall, 1961:222); and *rubiginosus* Wagner (1843:367) presumably occurring throughout the Amazonian lowlands to as far south as the Mato Grosso region of Brasil. On the basis of data from more than 1800 specimens of this species, I conclude that the geographic

FIGURE 21. Map showing selected distance coefficients (from the distance matrix) between localities from which specimens of *P. parnellii* were analyzed in the study of geographic variation. Symbols—circles, squares, triangles, and hexagons—correspond with particular couplets of the distance phenogram (Fig. 20). See text for key to localities.

variation, as expressed by cranial and external dimensions, is much more complex than implied by these names. Although this species is abundantly represented in museum collections, there still remains a serious paucity of material from several critical areas. Additional specimens and ecological data are needed from eastern Panamá, northern Colombia, and the northwestern portion of the Amazon Basin along the eastern margin of the Andes.

Relatively little is known about the ecology of these bats. From my limited experience in western and southern México, Nicaragua, and northeastern Venezuela, I think that *P. parnellii* has rather broad ecological tolerances. For example, at Palenque, Chiapas, this species was captured along trails cut through well-stratified, tropical deciduous forest. Near Santa Lucía, Sinaloa, specimens were caught in patches of deciduous forest that interdigitated with the oak and pine-oak forests of higher elevations. In western Nicaragua, *P. parnellii* was netted in xeric scrub forest on the Cosiqüina Peninsula and on the western portion of the Escudo Central in park-like savanna. In addition these bats are common in the humid Caribbean lowlands of eastern Nicaragua. The same range of arid to humid habitat also was noted in northeastern Venezuela.

Greatly simplified, the single most obvious trend in the geographic variation of the mainland representatives of

this species is an increase in external and cranial size, along with a less marked change in color from pale to dark, at progressively more southern latitudes (Fig. 19). Cranial and external size as well as color seem to be governed by yet poorly understood ecological factors. Apparently, *P. parnellii* as well as the entire genus *Pteronotus,* is mesophilic in habitat preference. In areas where there is a noticeable departure from the preferred humid tropical environment there is a concordant phenotypic expression of small size and pale color. In figure 20, the uppermost couplet—distinguished by a distance coefficient of 2.200—groups together populations of small-sized individuals of the entire subspecies *P. p. mexicanus,* a population from the northern part of the Yucatán Peninsula, and the Antillean populations from Cuba, Jamaica, and Puerto Rico. The remaining mainland populations of the species, which occupy more optimal tropical environments, are grouped (Fig. 20) by a couplet of lesser magnitude (distance coefficient, 2.000). However, within this group there are two distinct units that seem to correspond to the wet and dry extremes expressed in the environments of Middle and South America. (See figure 21 for selected distance coefficients between samples of *P. parnellii.*)

There are two distinct populations of *P. parnellii* south of the Isthmus of Tehuantepec in Middle America. One of these is described as a new subspecies and occupies northern Middle America and the Pacific versant. The other is a northern extension of *P. p. rubiginosus* from the Amazonian lowlands of South America and occupies the humid Caribbean versant from Central Honduras through eastern Panamá. In South America, there are two distinct populations; one of these as mentioned above is the Amazonian *P. p. rubiginosus.* The other, *P. p. fuscus,* is restricted to the semiarid Caribbean coast of Colombia and Venezuela and closely resembles the new subspecies from northern Middle America and the Pacific versant farther to the south (see account of *P. p. fuscus* for further discussion). Particular features of the geographic variation within and between the above-mentioned populations are considered in somewhat more detail in the accounts of the subspecies.

Key to localities used in statistical analysis of geographic variation.—1, Sonora; 2, northern Sinaloa; 3, Pánuco, Sinaloa; 4, vicinity of San Blas, Nayarit; 5, vicinity of Jamay and Chapala, Jalisco; 6, Colima; 7, southern Tamaulipas; 8, Cueva del Coyote, 6 km SSE Tonatico, México; 9, Cueva Poza de Montezuma, 1 km E Oaxtepec, Morelos; 10, vicinity of Teloloapan, Guerrero; 11, vicinity of Colotlipa, Guerrero; 12, Yerbabuena, Guerrero; 13, vicinity of San Andrés Tuxtla, Veracruz; 14, Teapa, Tabasco; 15, vicinity of Escárcega, Campeche; 16, southeastern Campeche; 17, northern British Honduras; 18, Gruta de Balankanche, 5 km E Chichén Itzá, Yucatán; 19, vicinity of Tehuantepec, Oaxaca; 20, vicinity of Arriaga and Tonalá, Chiapas; 21, vicinity of Tuxtla Gutiérrez, Chiapas; 22, vicinity of Palenque, Chiapas; 23, Cueva de Zapaluta, 1.3 mi SE Zapaluta, Chiapas; 24, La Democracia, Huehuetanango, Guatemala; 25, vicinity of San Cristóbal Verapaz, Alta Verapaz, Guatemala; 26, vicinity Las Quebradas, Izabal, Guatemala; 27, vicinity of Yepocapa, Chimaltenango, Guatemala; 28, Finca El Carnero, Jutiapa, Guatemala; 29, Las Flores Gracias, Santa Bárbara, Honduras; 30, vicinity of Comayagua, Comayagua, Honduras; 31, San José, Río Tinto, Olancho, Honduras; 32, vicinity of La Libertad, El Salvador; 33, vicinity of Divisadero, La Unión, El Salvador; 34, Estelí and Darío, Nicaragua; 35, vicinity of El Recreo, Zelaya, Nicaragua; 36, 3 mi S, 10 mi W Las Cañas, Guanacaste, Costa Rica; 37, Almirante, Bocas del Toro, Panamá; 38, Cerro Hoya, Los Santos, Panamá; 39, Penonomé, Coclé, Panamá; 40, Paraiso, Canal Zone, Panamá; 41, Bas Obispo, Canal Zone, Panamá; 42, Summit, Canal Zone, Panamá; 43, Cerro Azul, Panamá, Panamá; 44, Chilibre, Panamá, Panamá; 45, Buena Vista, Colón, Panamá; 46, Coloso, Las Campanas, Bolívar, Colombia; 47, Minas de Aroa, Bolívar R. R., Yaracuy, Venezuela; 48, vicinity of Urama, Yaracuy, Venezuela; 49, vicinity of San Esteban, Carabobo, Venezuela; 50, Curapao, 19 km E Caracas, Miranda, Venezuela; 51, northeastern (Sucre) Venezuela; 52, Isla de Margarita, Nueva Esparta, Venezuela; 53, Trinidad; 54, eastern Bolívar, Venezuela; 55, vicinity of Maripa,

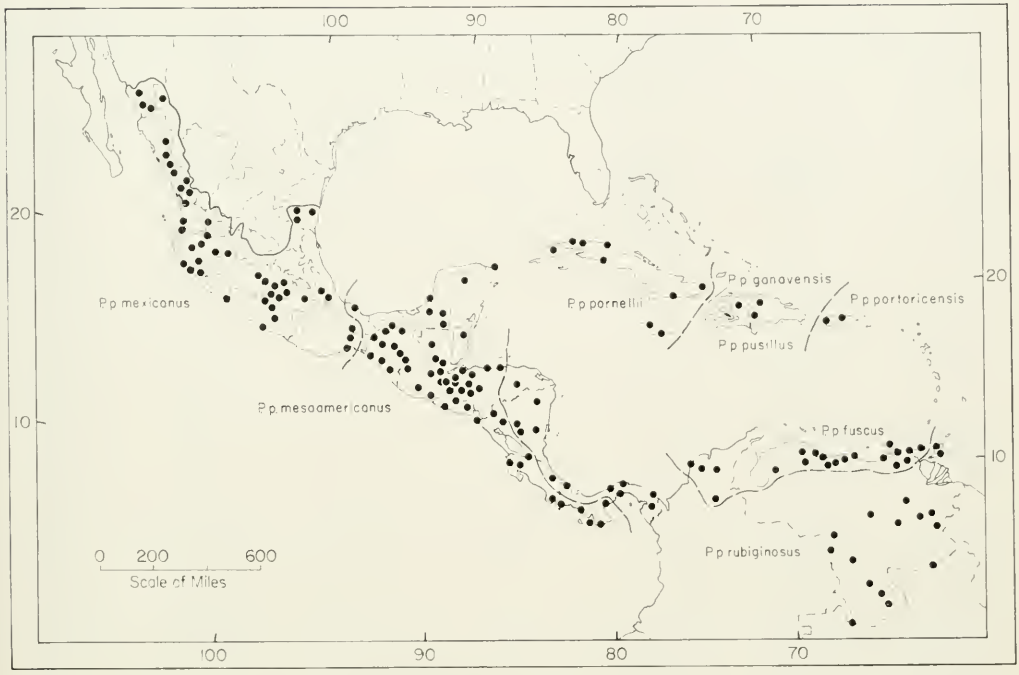


FIGURE 22. Distribution of *Pteronotus parnellii* in North America and northern South America. A few localities of record elsewhere in South America (Brasil, the Guianas, and Perú) are not shown (see account of *P. p. rubiginosus*).

Bolívar, Venezuela; 56, vicinity of Punto Páez, Apure, Venezuela; 57, Río Cunucununa, Belén, Amazonas, Venezuela; 58, Río Mavaca, 108 km SE Esmeralda, Amazonas, Venezuela; 59, Rio Negro, Serra de Cucuhy, Rio Bronco, Brasil; 60, vicinity of Tingo María, Huánuco, Perú; 61, Cuba; 62, Jamaica; 63, Hispaniola; 64, vicinity of En Café, La Gonave Island, Haiti; 65, Puerto Rico.

Pteronotus parnellii parnellii (Gray)

Phyllodia Parnellii Gray, 1843, Proc. Zool. Soc. London, p. 50, October.

Chilonycteris osburni Tomes, 1861, Proc. Zool. Soc. London, p. 66, May. Type locality, Sportsman Hall and Oxford Cave, Manchester, Jamaica; syntypes, BM 7.1.1.626 (male) and 7.1.1.632 (sex unknown).

Chilonycteris boothi Gundlach, 1861, Monatsb. k. preuss. Akad. Wiss., Berlin, p. 154. Type locality, "In Fundador, auch in Guines" [Matanzaz and Habana provinces, Cuba, respectively]; present disposition of holotype unknown.

Syntypes.—Two adults, sex unknown, skins, skulls not removed, BM 43.6.15.6-7; from unspecified locality in Jamaica; obtained by Richard Parnell.

Distribution.—Cuba and Jamaica (Fig. 22); no information presently available suggests that this race is limited to specific regions on either island, but future investigation may reveal such restriction.

Description.—Largest Antillean race both externally and cranially. Standard external measurements (average, with extremes in parentheses) of eight males and four females, respectively, from St. Clair Cave, St. Catherine Parish, Jamaica, as follows: total length, 79.4 (77.0-81.0); length of tail vertebrae, 20.4 (18.0-22.0); length of hind foot, 13.0 (13.0); length of ear from notch, 20.7 (20.0-22.0); see table 1 (localities 61 and 62), for additional selected external and cranial measurements.

The pelage is generally "tricolored" dorsally. As mentioned previously, color bands are not readily discernible, but three zones of color are more or less distinguishable. The basal fifth of the

TABLE 1. Selected external and cranial measurements of several populations of *Pteronotus parnellii*. Each measurement is represented by the observed range, below which is the mean, plus or minus two standard errors of the mean; superscript numbers indicate sample size if different from that given in left-hand colmun. See text for key to localities.

Locality	N	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
			Pteronotus parnellii mexicanus				
1	10	55.1±0.72[8]	11.6±0.18	7.5±0.14	8.6±0.13	18.9±0.17	8.9±0.12
		(53.3–56.3)	(11.0–11.9)	(7.2–7.9)	(8.2–9.0)	(18.5–19.3)	(8.6–9.2)
6	22	55.6±0.52	11.7±0.09[21]	7.6±0.07	8.8±0.07	19.3±0.15	8.9±0.09
		(53.1–57.9)	(11.3–13.1)	(7.4–8.0)	(8.5–9.2)	(18.8–20.0)	(8.4–9.3)
7	27	57.4±0.33[26]	11.8±0.09	7.6±0.08	8.8±0.05	19.5±0.09[26]	8.9±0.07
		(56.2–60.0)	(11.5–12.4)	(7.3–8.2)	(8.5–9.1)	(19.1–19.9)	(8.6–9.4)
8	14	58.1±0.64	11.8±0.11	7.7±0.09	8.8±0.06	19.4±0.12	9.1±0.05
		(55.2–59.4)	(11.5–12.1)	(7.4–8.0)	(8.6–9.0)	(19.1–19.8)	(8.9–9.3)
12	14	57.5±1.82	11.9±0.11[13]	7.8±0.08	8.9±0.10	19.5±0.15[13]	9.1±0.09[13]
		(55.3–59.7)	(11.4–12.1)	(7.6–8.0)	(8.6–9.3)	(19.0–20.6)	(8.8–9.4)
19	11	55.7±0.51	11.8±0.12	7.6±0.10	8.7±0.03	19.2±0.14	8.9±0.07
		(54.2–56.6)	(11.5–12.2)	(7.3–7.9)	(8.5–9.1)	(18.9–19.7)	(8.8–9.1)
			Pteronotus parnellii mesoamericanus				
20	11	58.7±1.95	12.4±0.12[10]	8.0±0.09	8.9±0.19	20.1±0.17[9]	9.3±0.12[10]
		(56.2–61.9)	(12.0–12.6)	(7.8–8.2)	(8.1–9.3)	(19.7–20.4)	(9.1–9.8)
15	13	58.3±0.51	12.2±0.12	7.9±0.10	9.0±0.07	19.7±0.14	9.1±0.13
		(56.5–59.7)	(12.0–12.4)	(7.6–8.1)	(8.9–9.2)	(19.4–20.1)	(8.8–9.3)
18	4	55.3±0.68	11.9±0.14	7.6±0.13	8.8±0.10	19.2±0.17	8.9±0.22
		(54.6–56.2)	(11.7–12.0)	(7.5–7.8)	(8.7–8.9)	(19.0–19.4)	(8.6–9.1)
27	14	58.7±0.54[11]	12.4±0.11	8.0±0.08	9.2±0.06	20.3±0.13	9.4±0.10
		(57.5–60.0)	(12.1–12.7)	(7.7–8.2)	(9.0–9.4)	19.8–20.7)	(9.0–9.7)
33	21	59.2±0.52[20]	12.3±0.07	8.0±0.09	9.2±0.06	20.3±0.11	9.4±0.07
		(57.4–61.2)	(12.1–12.7)	(7.6–8.4)	(9.0–9.5)	(20.1–20.9)	(8.9–9.6)
30	5	59.9±0.75	12.6±0.26	8.2±0.12	9.3±0.17	20.3±0.37	9.5±0.10
		(58.8–60.8)	(12.2–12.9)	(8.0–8.3)	(9.0–9.5)	(19.6–20.6)	(9.3–9.6)
38	19	59.5±0.59	12.7±0.12	8.2±0.05	9.4±0.07	20.5±0.10	9.5±0.10
		(56.8–61.9)	(12.3–13.2)	(7.9–8.4)	(9.1–9.5)	(20.2–21.2)	(9.1–10.0)
			Pteronotus parnellii rubiginosus				
31	9	60.2±0.75	12.6±0.12	8.3±0.09	9.4±0.11	20.9±0.13	9.6±0.08
		(58.7–61.6)	(12.3–12.8)	(8.1–8.5)	(9.2–9.7)	(20.6–21.2)	(9.4–9.8)
35	12	61.2±0.66[11]	12.9±0.17	8.3±0.12	9.6±0.09	20.9±0.18	9.7±0.09
		(59.6–63.0)	(12.4–13.3)	(8.0–8.6)	(9.3–9.8)	(20.3–21.3)	(9.4–9.9)
37	10	62.0±0.86	12.9±0.11	8.4±0.13	9.6±0.08	21.1±0.23	9.6±0.12
		(59.6–64.1)	(12.7–13.2)	(8.1–8.7)	(9.3–9.7)	(20.5–21.9)	(9.4–10.0)
40	26	61.0±0.39[19]	12.7±0.10	8.2±0.07	9.5±0.06	21.0±0.12	9.5±0.09
		(59.7–62.9)	(12.2–13.2)	(7.9–8.5)	(9.2–9.8)	(20.3–21.4)	(9.1–9.9)

TABLE 1. (Continued)

Locality	N	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
56	9	61.1±0.77 (59.5–62.8)	12.8±0.17 (12.4–13.2)	8.4±0.12 (8.1–8.7)	9.5±0.14 (9.2–9.7)	20.7±0.32 (19.6–21.1)	9.6±0.11 (9.5–9.9)
54	15	61.3±1.90[14] (58.4–64.3)	13.0±0.13[14] (12.6–13.3)	8.5±0.08 (8.3–8.8)	9.6±0.08 (9.5–9.9)	21.3±0.14[13] (20.9–21.7)	9.6±0.09[13] (9.4–9.9)
57	5	61.2±0.55 (60.7–62.2)	13.0±0.12 (12.8–13.1)	8.5±0.19 (8.2–8.7)	9.8±0.10 (9.6–9.9)	21.2±0.16 (21.0–21.5)	9.7±0.13 (9.5–9.9)
60	23	63.0±1.00[9] (60.2–65.4)	13.1±0.07 (12.7–13.4)	8.4±0.08 (8.0–8.8)	9.5±0.07 (9.1–9.7)	21.0±0.11 (20.5–21.6)	9.6±0.09 (9.1–10.0)
53	12	59.7±1.66[5] (58.3–61.6)	12.7±0.12[9] (12.5–13.0)	8.5±0.11[11] (8.3–8.8)	9.6±0.10 (9.3–9.9)	20.8±0.17[7] (20.4–21.0)	9.6±0.12[8] (9.4–9.8)
			Pteronotus parnellii fuscus				
46	15	59.7±1.83[14] (57.2–62.7)	12.5±0.13[12] (12.0–12.8)	8.3±0.05 (8.1–8.4)	9.4±0.06 (8.9–9.6)	20.4±0.13[13] (20.0–20.9)	9.4±0.10[12] (9.1–9.6)
49	19	59.9±0.67[15] (57.5–62.5)	12.3±0.12 (12.0–12.6)	8.0±0.08 (7.8–8.4)	9.2±0.06 (8.9–9.5)	20.3±0.18[18] (19.0–20.8)	9.3±0.05 (9.2–9.5)
51	10	59.8±0.62 (58.5–61.4)	12.5±0.20[9] (12.1–13.1)	8.3±0.11 (8.0–8.6)	9.3±0.11 (9.0–9.5)	20.5±0.20[9] (20.2–21.1)	9.4±0.16[8] (9.1–9.8)
52	15	58.0±0.52 (56.3–60.0)	12.1±0.13[14] (11.7–12.6)	8.1±0.07 (7.8–8.3)	9.2±0.08 (9.0–9.4)	20.3±0.13[12] (19.8–20.6)	9.2±0.09[14] (9.0–9.5)
			Pteronotus parnellii parnellii				
61	12	51.6±0.62[5] (50.0–52.5)	11.1±0.13[11] (10.8–11.6)	7.5±0.12 (7.2–7.9)	8.7±0.12 (8.2–9.0)	19.1±0.16 (18.7–19.4)	8.5±0.10[10] (8.3–8.8)
62	16	53.2±0.45[15] (51.7–54.7)	11.3±0.05[15] (11.1–11.5)	7.6±0.07 (7.4–7.8)	8.9±0.05 (8.7–9.1)	19.2±0.08 (18.9–19.6)	8.6±0.08 (8.1–8.8)
65	4	50.5±0.22 (50.2–50.7)	11.0±0.22 (10.8–11.3)	7.6±0.19[5] (7.3–7.8)	8.8±0.12[5] (8.6–8.9)	18.9±0.14 (18.8–19.1)	8.6±0.17 (8.3–8.7)
			Pteronotus parnellii pusillus				
64	2		10.1±0.10 (10.1–10.2)	6.6±0.07[5] (6.5–6.7)	7.5±0.08 (7.3–7.6)	16.4	8.1±0.18[3] (7.9–8.2)
			Pteronotus parnellii gonavensis				
63	8		10.2±0.13 (10.0–10.5)	7.0±0.11 (6.7–7.2)	7.9±0.08 (7.7–8.1)	17.5±0.23[7] (17.0–17.9)	8.2±0.12 (7.9–8.2)

individual hairs is dark brown (Prout's Brown) grading to a paler (whitish) central zone. The tips of the filaments are generally Snuff Brown. On top of the head, the central zone of the hairs expands and nearly obliterates the darker basal zone, imparting an overall pale appearance. Ventrally, the pelage on the pectoral and abdominal regions is sharply bicolored; the basal half of each hair is dark brown, whereas the terminal half is whitish. On the throat, the hairs are almost completely white or have a slight brownish cast.

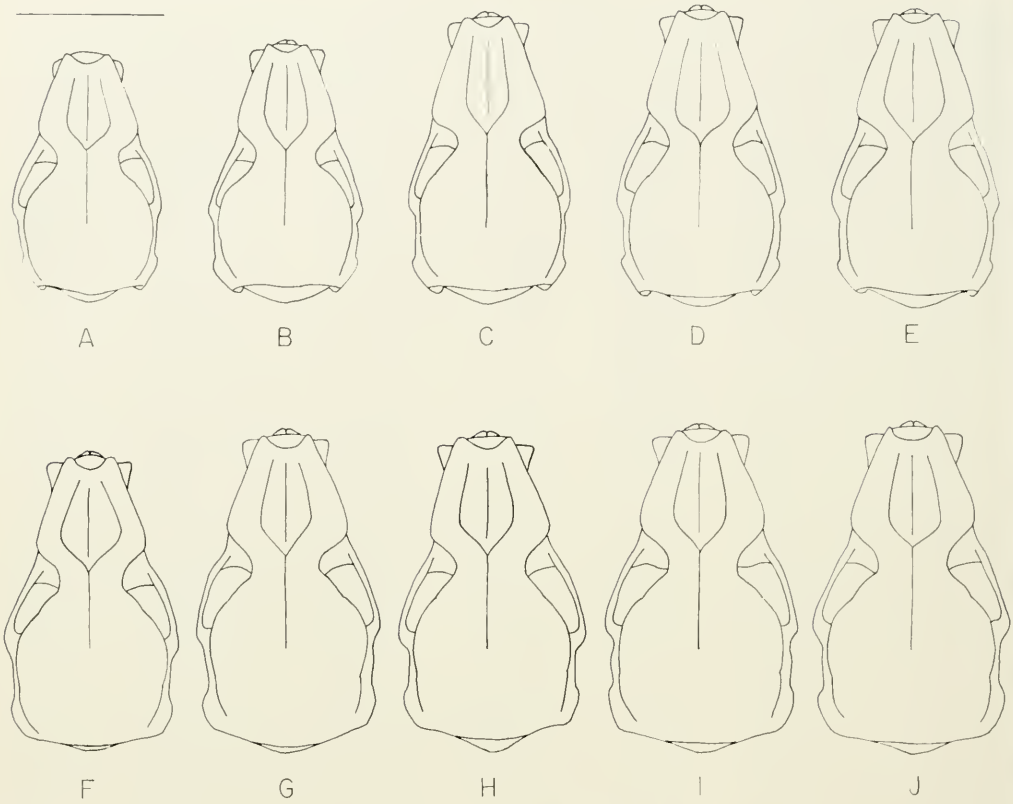


FIGURE 23. Dorsal views of skulls of *Pteronotus parnellii gonavensis* (A, La Gonave Island, Haiti), *P. p. pusillus* (B, Haiti), *P. p. portoricensis* (C, Puerto Rico), *P. p. parnellii* (D, Jamaica; E, Cuba), *P. p. mexicanus* (F, Sinaloa), *P. p. mesoamericanus* (G, Yepocapa, Guatemala), *P. p. fuscus* (H, Aroa, Venezuela), *P. p. rubiginosus* (I, Bonanza, Nicaragua; J, Maripa, Venezuela). All specimens are adult males; horizontal line above A is 10 mm in length.

Comparisons.—For comparison with *P. p. portoricensis* see account of that subspecies. From both *P. p. pusillus* and *P. p. gonavensis*, *P. p. parnellii* is easily distinguished on the basis of larger external and cranial size (Table 1). In addition, the rostra of both *pusillus* and *gonavensis* are relatively shorter and broader than that of *parnellii* (Fig. 23).

Remarks.—J. Knox Jones, Jr., kindly examined the syntypes of *Chilonycteris osburni* Tomes, 1861; although the length of the forearm (52.3 in each) is slightly smaller than usual, they are clearly within the range of variation of Jamaican *P. p. parnellii*.

There is nothing in Gundlach's (1861:154-155) description of the Cuban *Chilonycteris boothi* that clearly diagnoses that taxon. Peters (1872:360) and Dobson (1878:452) synonymized both *osburni* and *boothi* under *Chilonycteris parnellii*. On the other hand, Miller (1902:401) compared *portoricensis* with both *parnellii* and *boothi*, which he recognized as distinct species. Miller alleged that the lower premolars were so crowded in *parnellii* that the second premolar was excluded lingually from the toothrow, and the first and third premolars were in contact, but that crowding was not particularly apparent in either *boothi* or *portoricensis*; the latter was further distinguished on the basis of shorter ears. Miller (1904:341-342) reiterated the differences between Cu-

ban *boothi* and Jamaican *parnellii,* but also stated that otherwise the two species were "closely similar." Rehn (1904: 197) was the first to apply *boothi* as a trinomen. In addition to Miller's characteristics of the lower premolars, Rehn further distinguished the Cuban bats by a "more depressed rostrum and the more robust form." After studying these two insular populations, it is apparent to me that the degree of crowding of the lower premolars is variable and that there are no marked differences in the "depression" of the rostrum. Therefore, because of the great degree of overlap in external and cranial dimensions (Table 1), I regard *Chilonycteris boothi* Gundlach, 1861, as a junior synonym of *P. p. parnellii* Gray, 1843.

Specimens examined (62).—CUBA. *Habana:* Cueva de Cotilla, 4 mi S San José de Las Lajas, 2 (AMNH); Cueva de Numancia, Aguacate, 2 (AMNH). *Las Villas:* Cueva del Agua, Sagua La Grande, 5 (ROM); Cueva de Los Masones, Trinidad, 1 (ASC). *Oriente:* Cueva de Las Majaes, Caney, 6 (1 AMNH, 5 ROM); Baracoa, 4 (USNM). *Pinar del Río.* San Vicente, 1 (ASC); *Pan de Guajaibon,* 1 (AMNH). JAMAICA. *Hanover:* Lucca, 3 (AMNH). *St. Catherine:* Healthshire Hills Caves, 1 (AMNH). *St. Elizabeth: Wallingford Cave, near Balaclava,* 4 (AMNH); *Oxford Cave, near Balaclava,* 10 (AMNH); *Perú Cave, near Goshen,* 1 (AMNH); *St. Clair Cave,* 12 (ROM). *Trelawny:* Windsor Cave, 7 (2 AMNH, 5 ASC). No specific locality, 2 (USNM).

Pteronotus parnellii pusillus (G. M. Allen)

Chilonycteris parnellii pusillus G. M. Allen, 1917, Proc. Biol. Soc. Washington, 30:168, 23 October.

Holotype.—Adult female, skin and skull, MCZ 16468; from Arroyo Salado, Dominican Republic, Hispaniola; obtained by James L. Peters on 7 March, 1916.

Distribution.—Haiti and Dominican Republic (Fig. 22).

Description.—Size, smallest of races of *parnellii* definitely still living, both externally and cranially. Standard external measurements for an adult female from Cueva Durán, 4 km SW Monción, Dominican Republic, are as follows: total length, 73; length of tail vertebrae, 20; length of hind foot, 12; length of ear from notch, 18; length of forearm of three adult females, 48.9, 50.2, and 50.5. Additional selected cranial measurements of combined material from Haiti are given in table 1 (locality 64). Viewed in profile, the forehead of *pusillus* rises more abruptly and the braincase is shorter and more globular than in other Antillean races, except *P. p. gonavensis* (Fig. 23).

The color of the pelage is Snuff Brown dorsally becoming paler on the head and nape. Like *P. p. parnellii* there is a discernible central zone on the individual filaments of hair from the back. Ventrally, the pectoral and abdominal regions are brown with a drab wash, becoming paler on the throat.

Comparisons.—This race is easily distinguished from all other subspecies (mainland and insular) except *P. p. gonavensis,* purely on the basis of external and cranial size. From *P. p. gonavensis,* the subspecies *pusillus* is recognizable by larger cranial size (Table 1, see especially length of maxillary toothrow, and condylobasal length). Furthermore, *pusillus* has a relatively longer, narrower rostrum (Fig. 23).

Remarks.—The distinctness of *P. p. pusillus* and *P. p. gonavensis* from all other races of *parnellii* is represented by a distance coefficient of 7.800 (Fig. 20). The magnitude of this coefficient, in comparison to those between other populations of *parnellii,* is so great that *pusillus* and *gonavensis* might well represent distinct species. The relationships between these two taxa and the larger Antillean races *(parnellii* and *portoricensis)* are not clearly understood and, as will be discussed beyond, the evolutionary and zoogeographic relationships of the larger subspecies also are poorly known. In view of these considerations, and because *pusillus* and *gonavensis* resemble *parnellii* morpho-

logically, I here retain them as subspecies of the latter.

Specimens examined (15).—HAITI. San Michel, 6 (USNM); *Diquini,* 1 (USNM); *San Raphael,* 1 (USNM). DOMINICAN REPUBLIC. *María Trinidad Sanchez:* Arroyo Salado, 2 (MCZ). *Samana:* Cave near Sanchez, 1 (USNM). *San Juan:* Rancho La Guardia, 1 (AMNH). *Santiago Rodriguez:* Cueva Durán, 4 km SW Monción, 3 (1 AMNH, 2 ROM).

Pteronotus parnellii gonavensis (Koopman)

Chilonycteris parnellii gonavensis Koopman, 1955, Jour. Mamm., 36:110, 25 February.

Holotype.—Cranium only, lacking incisors and auditory region, USNM 295009; from an owl pellet deposit found in a cave near En Café, La Gonave Island, Republic of Haiti, Hispaniola; collected by A. J. Poole and W. M. Perrygo in March 1929.

Distribution.—Known only from type locality as a sub-Recent fossil (Fig. 22).

Description.—Size, cranially the smallest known subspecies of *P. parnellii*; see table 1 (locality 63) for selected cranial measurements. Rostrum noticeably short (Fig. 23); forehead rising abruptly over short, rounded braincase as in *P. p. pusillus.*

Comparisons.—As mentioned in the previous account, *P. p. gonavensis* is easily distinguished from all other races of *parnellii,* except *pusillus,* solely on the basis of being smaller cranially. From *pusillus,* it differs in having a shorter, broader rostrum, and generally shorter, slightly narrower skull (Fig. 23).

Remarks.—This subspecies is based entirely on subfossil material from an owl pellet deposit found in a cave on La Gonave Island, which is located in the Gulf of Gonaïves off western Hispaniola. This subspecies is closely related to the Hispaniolan subspecies *pusillus.* In addition to cranial remains, Koopman (1955:112) reported the presence of *pusillus*-like radii in the En Café material. These wing elements were, however, slender in comparison to those of *pusillus* from St. Michel, Haiti. A case could be made for elevating *pusillus* to specific rank, in which event *gonavensis* should remain associated with *pusillus* as a distinct subspecies.

Specimens examined (11).—HAITI. Cave near En Café, La Gonave Island, 11 (USNM).

Pteronotus parnellii portoricensis (Miller)

Chilonycteris portoricensis Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54:400, 12 September.

Holotype.—Adult female, skin and skull, USNM 102358; from cave near Pueblo Viejo [Cueva di Fari], Puerto Rico; obtained by L. Stejneger and C. W. Richmond.

Distribution.—Known only from Puerto Rico (Fig. 22).

Description.—Size, only slightly smaller, both externally and cranially, than *P. p. parnellii* from Cuba and Jamaica. Standard external measurements of two males from Cueva Trujillo Alto are as follows: total length, 78, 83; length of tail vertebrae, 20, 20; length of hind foot, 12, 13; length of ear from notch, given as 19 and 21 by Miller (1902:401); see table 1 (locality 65) for additional selected external and cranial measurements. It is impossible to describe the color of the pelage of this subspecies because most of the material examined was preserved in spirits and badly bleached. Miller (1902) and Rehn (1904) suggest that the color is not greatly different from that of *P. p. parnellii.*

Comparisons.—From both *P. p. pusillus* and *P. p. gonavensis,* this subspecies can be recognized by larger cranial size (Fig. 23). The differences between *portoricensis* and *parnellii* of Cuba and Jamaica are less striking in that *portoricensis* averages only slightly smaller than *parnellii* (Figures 19, 23, and Table 1).

Remarks.—In his description of *Chilonycteris portoricensis,* Miller (1902:

401-402) noted its close resemblance to *Chilonycteris boothi* (=*P. p. parnellii*) from Cuba; the former being characterized by short ears. However, there is nothing in my data to suggest any differences in the length of the ears of these two geographically separated populations.

Several points must be considered in order to interpret the observed similarity between *parnellii* and *portoricensis*. The problem would be less complex if Cuba, Jamaica, and Puerto Rico were adjacent islands. However, the island of Hispaniola, through which gene flow should logically pass, is geographically interposed between Puerto Rico and the other two islands. Furthermore, the Hispaniolan subspecies *pusillus* as well as *gonavensis* are notably dissimilar from all other Antillean races of *P. parnellii* (Fig. 21) and cannot be construed to represent intermediates in a continuum between the populations of the islands in question. It is of course possible, owing to an inadequate knowledge of the Hispaniolan bat fauna, that there is an as yet undiscovered population of more typical *parnellii*-like bats on Hispaniola. On the other hand, the similarities between *parnellii* and *portoricensis* may have been independently acquired, or perhaps these two represent the primitive condition of the Antillean *parnellii* stock from which *pusillus* was derived. Until the situation is better understood, I elect to recognize the Puerto Rican population as a distinct subspecies.

Specimens examined (7).—PUERTO RICO. Pueblo Viejo, 1 (USNM); *Cueva di Fari near Pueblo Viejo*, 4 (USNM); Cueva de Trujillo Alto, 2 (AMNH).

Pteronotus parnellii mexicanus (Miller)

Chilonycteris mexicana Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54:401, 12 September.

Pteronotus parnellii mexicana Hall and Dalquest, 1963, Univ. Kansas Publ. Mus. Nat. Hist., 14:217, 20 May.

Holotype.—Adult male, skin and skull, USNM 89277; from San Blas, Nayarit; obtained by E. W. Nelson and E. A. Goldman on 9 June, 1897; original no. 11132.

Distribution.—México, north of the Isthmus of Tehuantepec along the Pacific lowlands to central Sonora (Cueva de la Tigre, 15 mi SSE Carbó, Cockrum and Bradshaw, 1963:3) and north along the Gulf coast to southern Tamaulipas (Sierra de Tamaulipas, 2 mi S, 10 mi W Piedra); also known from subtropical regions of the plateau states of Chihuahua, Durango, and San Luis Potosí (Fig. 22).

Description.—Size small for a mainland race of the species, both externally and cranially. Standard external measurements (average, with extremes in parentheses) of eight males and five females, respectively, from 2 mi SE Jalcocotán, 3000 ft, Nayarit, are as follows: total length, 89.2 (88.0-94.0), 89.9 (83.0-90.0); length of tail vertebrae, 21.6 (20.0-24.0), 21.0 (19.0-22.0); length of hind foot, 13.6 (13.0-14.0), 13.8 (13.0-14.0); length of ear from notch, 22.0 (21.0-23.0), 21.6 (21.0-22.0). See table 1 (especially localities 1, 6, and 7), for additional selected external and cranial measurements.

The pelage of mainland subspecies of *Pteronotus parnellii* is less distinctly tricolored dorsally than that of insular races. A nearly monocolored pelage results primarily from a weak expression of the whitish central zone on the hairs of the back; in *P. p. mexicanus*, this central zone is Cinnamon-Buff with basal and terminal portions brownish. Specimens examined from near the type locality and from western México are noticeably paler (Snuff Brown) in color than those of other mainland races. The head and nape are the same color. Ventrally, the pectoral and abdominal regions are pale drab gray with a buffy tinge, becoming slightly paler on the throat and chin.

Comparisons.—For comparison with

the adjacent subspecies in Middle America, see the following account. From the Antillean races *P. p. parnellii* and *P. p. portoricensis,* the subspecies *mexicanus* is distinguishable by its larger size, both externally and cranially (Table 1), and less strikingly tricolored pelage. The breadth and length of the skull are greater in *mexicanus* than in any of the Antillean populations (Fig. 23).

Remarks.—Unlike insular areas, zones of intergradation are more easily discernable on the mainland where continuous gene flow obtains in the absence of barriers. The typical population of *P. p. mexicanus* inhabits western México; bats of this race become progressively larger (Table 1) and darker as they approach the region of the Isthmus of Tehuantepec. A rather narrow zone of intergradation seems to exist in this region between *mexicanus* and the subspecies in southern México and northern Middle America. Trans-isthmian resemblances, based on distance coefficients (Fig. 21), are greater in the north and central parts of the Isthmus than along the southern, Pacific portion. In fact, bats from the Sierra de Los Tuxtlas resemble those from Guatemala to such an extent as to justify their assignment to the same subspecies. The large distance coefficient (2.077) between localities 19 and 21 (Fig. 21) may reflect the relatively more arid conditions which could constitute a partial barrier in that part of the Isthmus. The northern part of the Isthmus may act less like a barrier to gene flow due to the more mesic conditions in that region. The influence of such gene flow seems to extend along the eastern coast of México with representatives of *mexicanus* being slightly larger and somewhat darker than those in western México. The darkness of Tamaulipan specimens described by Alvarez (1963:398) is related to seasonal change of color.

As mentioned previously, small size and pale color probably relate to some, as yet poorly understood, factors of the suboptimal environment in which some *parnellii* live. In addition, the composition of the insectivorous chiropteran fauna and intraspecific competition may have influenced the evolution of *P. p. mexicanus* in western México as well as the Antillean races. In the Pacific lowlands of Sinaloa, there are 20 to 25 species of insectivorous bats, including other mormoopids *(Pteronotus personatus, P. davyi* and *Mormoops megalophylla).* The majority of these species are small, slow-flying bats that probably do not directly compete with *P. p. mexicanus* (or other mormoopids, for that matter). However, at least eight (primarily molossids and lasiurines) are large, swift-flying bats that may compete directly with *P. p. mexicanus* and other mormoopids. In this arid subtropical habitat, where environmental stresses may be more stringent on prey and predator, the more temperate species may have a selective advantage over the mormoopids that also inhabit the region. Therefore, in such regions, smaller size in *P. parnellii* could be in response to this competitive pressure. In more tropical environments, although the total number of insectivorous bats may increase, there are comparatively fewer large, swift-flying species.

Specimens examined (460).—MEXICO. *Chihuahua:* Carimeche, Río Mayo, 10 (UMMZ); *1.5 mi SW Tocuina, 1500 ft,* 1 (KU). *Colima:* Playa de Oro, 8 km W, 2 km S Santiago, 1 (KU); 3 mi S Santiago, 1 (KU); *7 mi W, 0.5 mi S Santiago,* 15 (KU); *4 km S Coquimatlán,* 5 (LACM); *Pueblo Juárez,* 6 (LACM); *Rancho Tabarnillas, 6 km N Agua Zarca,* 6 (IB); *North Slope La Media-Luna,* 8 (LACM). *Distrito Federal:* Wards Natural History Establishment (presumably Tacubaya, D. F.), 2 (USNM). *Durango:* Santa Ana (12 km E Cosalá, Sinaloa), 1300 ft, 2 (KU). *Guerrero:* 12 km N Zacatula, 6 (ENCB); Puente de Dios, Yerbabuena, 1700 m, 16 (KU); *Cueva Laguna Honda, Yerbabuena,* 12 *km NNW Teloloapan, 1800 m,* 4 (IB); *Ojo de Agua de Mexicapan, 4.3 km N Teloloapan, 1480 m,* 4 (IB); *Puente de Los Sabinos, 16 km E Teloloapan, 1040 m,* 5 (IB); *Ojo de Agua de Chapa, 5 km SE Teloloapan, 1520 m,* 14 (IB); *10 mi E, 2 mi S Teloloapan,* 1 (KU); Grutas Cacahuamilpa, 4 (ENCB); 3

mi W Mexcala, 2000 ft, 3 (TCWC); *3 km N Agua de Obispo, Chilpancingo,* 1 (KU); *1 mi N, 6 mi E Tuxtla,* 2 (TCWC); *Grutas de Juxlahuaca, 5 km N Colotlipa, 800 m,* 3 (TCWC); *4 km NE Colotlipa, 1100 m,* 11 (ENCB); 2 mi NW Acapulco, 50 ft, 8 (KU). *Jalisco:* Bolaños, 1 (USNM); 1.5 mi WNW Amatitan, 4100 ft, 1 (KU); 15 km W Ameca, 4200 ft, 3 (KU); 10 mi SE Talpa de Allende, 5350 ft, 1 (KU); El Zapote, 3 (IB); *5 mi W Chapala, 5000 ft,* 13 (KU); 4 mi SE Ocotlán, 4 (MCZ); *0.5 km N, 3 km W Jamay, 1650 m,* 26 (7 ENCB, 19 IB); 5 mi S Grullo, 3100 ft, 1 (KU); *6 mi E Limón, 2700 ft,* 3 (KU); 15 km NW Cihuatlán, 3 (KU). *México:* 7.5 km S, 10 km E Valle de Bravo, 2100 m, 2 (ENCB); Cueva del Coyote, 6 km SSE Tonatico, 1500 m, 16 (AMNH). *Michoacán:* 5 km SW Turandeo, 1900 m, 7 (ENCB). *Morelos:* Cueva Poza de Montezuma, 1 km E Oaxtepec, 1450 m, 32 (IB); 0.5 mi NW Huajintlán, 3410 ft, 2 (TCWC). *Nayarit:* San Blas, 7 (1 MVZ, 6 USNM); *8 mi E San Blas,* 7 (LACM); *2 mi SE Jalcocotán, 3000 ft,* 13 (KU); 6 mi SSE Las Varas, 3 (KU). *Oaxaca:* 3 km WNW Dominguillo, 730 m, 5 (KU); 13 mi E Juchitán, Isthmus of Tehuantepec, 1 (LACM); *Tehuantepec,* 1 (USNM); *6 mi NW Mixtequilla,* 8 (TCWC); *18 mi N Matías Romero,* 1 (LACM); *8 km NW Salina Cruz,* 11 (ENCB); *Huilotepec,* 1 (USNM). *Puebla:* 1 mi E Raboso, 4350 ft, 1 (KU); *1 mi SE Raboso,* 14 (KU). *Sinaloa:* 12 mi NE San Benito, 1000 ft, 1 (KU); *20 km N, 5 km E Badiraguato, 1800 ft,* 1 (KU); 23 km W Pericos, 1 (LACM); 4 mi S Casa Blanca, 1200 ft, 1 (KU); 3 mi SE Camino Real, 500 ft, 10 (KU); 1.5 km W Copala, 1400 ft, 4 (KU); *Pánuco, 22 km NE Concordia, 2050 ft,* 33 (KU); *1 mi E Santa Lucía, 3650 ft,* 2 (KU); *Rancho Batel, 6 mi E Santa Lucía, 6300 ft,* 2 (LACM); *1.5 km S Santa Lucía, 3200 ft,* 11 (KU); *2.5 mi NE Concordia,* 1 (KU); *1.5 mi E Concordia, 250 ft,* 2 (MSU); *12 mi N Villa Unión, 400 ft,* 3 (KU); *15 mi N Rosario, Chele, 300 ft,* 1 (UMMZ); 5 mi WSW Plomosas, 800 ft, 3 (KU); 0.5 mi S Concepción, 250 ft, 1 (KU). *Sonora:* 1 mi E Buena Vista, on Río Yaqui Reservoir, 1000 ft, 1 (KU); Tésia, between Navajoa and Camoa, 7 (AMNH); Alamos, 1 (ROM); *Prothonatorio Mine, 3 mi W La Aduana,* 1 (LACM); *0.25 mi W Aduana, 600 ft,* 3 (KU); *Aduana, 4 mi SW Alamos,* 2 (CAS); no specific locality, 1 (KU). *Tamaulipas:* Sierra de Tamaulipas, 2 mi S, 10 mi W Piedra, 1200 ft, 1 (KU); *Sierra de Tamaulipas, 3 mi S, 16 mi W Piedra, 1400 ft,* 3 (KU); *10 km N, 8 km W El Encino, 400 ft,* 22 (KU); *Rancho Pano Ayuctle, 25 mi N El Mante, 3 km W Pan American Highway, 300 ft,* 3 (KU); *Ojo de Agua, 20 mi N El Mante, 3 km W Pan American Highway, 300 ft,* 2 (KU); 7 mi W Ocampo, 2400 ft, 1 (KU). *Veracruz:* Mirador, 2 (USNM); 8 km NW Poterero, 1700 ft, 1 (KU); 38 km SE Jesús Carranza, 500 ft, 2 (KU).

Pteronotus parnellii mesoamericanus new subspecies

Holotype.—Adult male, skin and skull, KU 64713; from 1 mi S and 0.75 mi E Yepocapa, 4280 ft, Chimaltenango, Guatemala; captured by James W. Bee and J. A. Ibarra on 7 January 1955; original no. 550107-31 of Bee.

Distribution.—México south of the Isthmus of Tehuantepec, including Sierra de Los Tuxtlas and the Yucatán Peninsula, westward into Guatemala, British Honduras, and El Salvador to central Honduras (west of Sierra de Esperanza), thence southward along the Pacific versant of Nicaragua and Costa Rica to the Province of Coclé, west of the Cordillera de Talamanca, in western Panamá (Fig. 22).

Description.—Size medium, both cranially and externally, for mainland races of *parnellii.* Standard external measurements for the holotype, followed by the average (extremes in parentheses) for 11 males and 29 females respectively, from the type locality are as follows: total length, 96, 95.6 (93.0-98.9), 95.9 (93.0-98.0); length of tail vertebrae, 26, 24.5 (23.0-26.0), 24.5 (23.0-27.0); length of hind foot, 14 for all specimens of series; length of ear from notch, 22, 21.8 (21.0-22.0), 21.5 (20.0-22.0). Additional selected external and cranial measurements are given in table 1 (see especially localities 27 and 33).

Individuals in the series from the type locality, all obtained in early January, are not in fresh pelage; all are dark brown (near Prout's Brown) dorsally. There is no marked change in the color of the pelage on the nape and head. Ventrally, in the pectoral and abdominal regions, the basal portion of the hairs are nearly Prout's Brown giving an overall dark brown appearance to the pelage; the tips of the hairs are

pale Cinnamon-Buff and give a "frosted" appearance to the venter; the throat and chin regions usually are somewhat paler. Specimens captured in early March from near Chinajá and Toocog, Petén, Guatemala, are in fresh pelage and are somewhat darker than those from the type locality. Three December-taken males from Puente Punta Gordo, Guatemala, are brilliant Ochraceous Tawny in color, both dorsally and ventrally.

Comparisons.—From *P. p. mexicanus*, the new subspecies can be distinguished by larger external and cranial size (Table 1). This is especially true in comparison with specimens of *mexicanus* from the northern parts of its range; individuals of *mexicanus* are generally paler in color.

Compared with *P. p. rubiginosus*, *P. p. mesoamericanus* averages smaller in size, both cranially and externally. The color of *mesoamericanus*, although darker on the average than that of *mexicanus*, is paler compared to the pelage of *rubiginosus*. In the zone of intergradation between *mesoamericanus* and *rubiginosus*—eastern Honduras, southward more or less along the continental divide—these two races become increasingly more difficult to distinguish. As a rule, bats from the Pacific versant, although increasing somewhat in overall size in Panamá, are usually smaller and paler than bats of the Caribbean coastal lowlands, herein assigned to *rubiginosus*.

Remarks.—Specimens assigned to this new subspecies have been variously referred to in the past as *Chilonycteris parnellii fusca* (Koopman, 1955; Hall and Kelson, 1959; Ryan, 1963), *Chilonycteris rubiginosa fusca* (Hershkovitz, 1951; Felten, 1956), and *Pteronotus parnellii fuscus* (Jones, 1966 and Jones, *et al.* 1971). The relationship between *fuscus* and *mesoamericanus* will be considered in more detail below.

Typical populations of *mesoamericanus* are found in south-central Guatemala, and *mesoamericanus* gradually intergrades with *mexicanus* in northern Chiapas, Tabasco, and southern Veracruz. As was mentioned earlier, gene flow between these two races evidently decreases, probably owing to adverse ecological conditions, across the southern Pacific coast of the Isthmus of Tehuantepec (see figure 21 for distance coefficients). In a similar fashion, southern populations of *mesoamericanus* become involved in a zone of intergradation with *rubiginosus*. These trends are normal and expected in continuous, freely interbreeding populations of the same species. On the Yucatan Peninsula there is a marked reduction in external and cranial size at progressively more northern localities which can easily be seen by comparing localities 20, 15, and 18 (Table 1). Furthermore, it will be noted that localities 15, 16, and 17 become increasingly more distinct from locality 18. This trend seems to be related to the increasingly suboptimal or xeric conditions on the northern part of the peninsula. Perhaps ecological factors that influence this "peninsular effect" are similar and independently involved in the small size and pale color of typical *mexicanus* in western México. Another instance in which reduced size and pale color seem to be correlated with xeric conditions occurs in *P. p. fuscus* from Margarita Island off the northeastern coast of Venezuela.

There are several important aspects concerning the zone of intergradation between *mesoamericanus* and *rubiginosus*. First, geographically distinct populations of *P. parnellii* appear to be segregated into east and west versants in Middle America. This situation is by no means novel, having been recognized by herpetologists for some time; recently Davis (1968, 1969, and 1970) considered geographic variation in *Uroderma* and *Artibeus* from this point of view. Ryan's (1963) Biotic Provinces of Central America, based on mammalian distributional patterns, also reflect Pacific and Caribbean versants. The distinct-

ness of populations occupying these versants no doubt depends a great deal on the ecological tolerance of the particular species. In the case of *P. parnellii*, the versants seem to have had a moderate effect in the differentiation and isolation of *mesoamericanus* and *rubiginosus*.

Secondly, the size and shape of the landmass in relationship to the ecology and proximity of the two versants to each other seems to play an important role in their overall effectiveness. The Middle American landmass is widest in southern Honduras and northern Nicaragua, and gradually becomes wedge-shaped in northern Costa Rica. From this point southward to northern South America, the landmass is extremely narrow. The transverse mountain masses in central Honduras and northern Nicaragua seem to form a partial barrier between *mesoamericanus* to the north and west and *rubiginosus* to the southeast. However, south of this mountain mass, the versants with their corresponding populations of *P. parnellii* are separated only by a broad ecotonal belt and in some places by mountains. Gene exchange may take place more or less freely across this landmass. The small size of *mesoamericanus* in northwestern and central Nicaragua (as compared to the larger *rubiginosus* of the Miskito lowlands of eastern Nicaragua) seems to be an indication of the relative effectiveness of the broad ecotone in maintaining the two subspecies where interposed mountainous areas are lacking. As the landmass becomes increasingly narrower there is a concurrent reduction in the breadth of the ecotone and the two versants come into closer proximity. The overall effect is the development of a broader zone of intergradation in which both versant populations of *P. parnellii* become gradually larger in size, but with *mesoamericanus* always averaging slightly smaller.

In eastern Panamá and northwestern Colombia (the area from the Canal Zone to the Bolívar Geosyncline) the zone of intergradation between *mesoamericanus* and *rubiginosus* becomes more complex with the incorporation of gene flow from western populations of *P. p. fuscus*. Phenotypically, *rubiginosus* dominates the intergradation in this region. *Pteronotus p. rubiginosus* is continuous from eastern Nicaragua to the Amazon Basin and effectively separates *P. p. fuscus* and *P. p. mesoamericanus*, which are similar in appearance and indeed may be closely related (see account of *P. p. fuscus*).

Dunn (1940:156), reporting on the herpetofauna of Panamá, noted what he called a "faunistic crossing over" in the Canal Zone and Darién. This idea was founded on apparent affinities between the fauna that occurs in the Pacific versant of Panamá and that of the Caribbean coast of South America; the fauna of the wetter Atlantic side (Caribbean versant) reportedly had its closest affinities with the fauna of the Pacific coast of Colombia. Although, this apparent "crossover" has not yet been clearly defined for mammals, it is strongly suggested in this analysis of geographic variation of *P. parnellii*. A somewhat similar situation seems to exist in Davis's (1968, 1969, and 1970) data for *Uroderma* and *Artibeus*. I suspect that with further investigation this pattern of distribution may be found to be relatively common among bats as well as other small mammals.

Haffer (1967a, 1967b and 1970), in his study of the zoogeography of the Colombian bird fauna, discussed the probable effects of climatic changes during the Pleistocene on the tropical forests of Central America and northern South America. With alternating wet glacials and dry interglacials, Haffer suggested an alternating expansion and contraction of tropical forests in this vast region. In eastern Panamá and northwestern Colombia, each of these circumstances would have allowed for a differential continguity between Middle

American populations of *P. parnellii* and those of South America and thus a differential in gene flow at different times. During dry climatic periods, when the tropical forest contracted into respective Middle and South American nuclei, gene flow between populations of *P. parnellii* from the Pacific versant of Middle America and the Caribbean coast of northern South America no doubt prevailed through the narrow causeway in eastern Panamá. On the other hand, with wet climatic periods and resultant expansion of tropical forest, the above-mentioned gene flow could have been cut off or at least replaced by panmixia between populations of *P. parnellii* from the Caribbean versant of Middle America and those of the Amazon Basin.

The subspecific name *mesoamericanus* was selected to describe the geographic region of Middle America in which bats of this subspecies live.

Specimens examined (517).—MEXICO. *Campeche:* 5 km S Champotón, 1 (KU); *1 km N, 13 km W Escarcéga, 65 m,* 7 (KU); *12 km W Escarcéga,* 7 (KU); *7.5 km W Escarcéga, 65 m,* 3 (KU); 105 km E Escarcéga, 1 (KU); *103 km SE Escarcéga,* 7 (KU); 65 km S, 128 km E Escarcéga, 4 (KU). *Chiapas:* 10 km N, 1.5 km E Raudales, 150 m, 3 (ENCB); *16 mi NW Palenque, 100 ft,* 1 (TCWC); *Ruinas de Palenque, 140 m,* 4 (ENCB); 21 km WSW Teapa, 200 ft, 1 (TCWC); *approx. 8 km S Solosuchiapa, 400 ft, (Camp on Río Teapa),* 1 (LACM); 12 mi W Mal Paso, 400 ft, 2 (TCWC); 7 mi WSW Ocozocoautla, 2500 ft, 2 (TCWC); *Cerro Hueco Cave, 2 mi SE Tuxtla Gutiérrez, 266 ft,* 5 (TCWC); *2 mi S Tuxtla Gutiérrez,* 2 (MCZ); *4 mi NE Chiapa de Corzo, 3000 ft,* 6 (TCWC); *6 mi SE San Cristóbal, 7300 ft,* 2 (MVZ); Cueva de Zapaluta, 1.3 mi SE Zapaluta, 5700 ft, 53 (TCWC); 2 km NW San Lucas, 3300 ft, (33 km SE Zapaluta), 3 (TCWC); 7 km W Los Amates, 1800 ft, 5 (TCWC); *Finca Oquilapa, 8 mi SE Tonalá, 100 ft,* 3 (LACM); *15 km SE Tonolá, 100 ft,* 6 (TCWC); 5 km SE Pijijiapan, 100 ft, 5 (TCWC); 11 km NW Escuintla, 100 ft, 4 (LACM). *Quintana Roo:* Aeropuerto, 4 km WSW Puerto Juárez, 5 m, 1 (KU). *Tabasco:* 2 mi SW Teapa, 1 (KU); *5 mi SW Teapa,* 9 (KU). *Veracruz:* Río Basura, 3 km N Zontecomapan, 2 (ENCB); *Zontecomapan,* 4 (ENCB); *2 mi WNW San Andrés Tuxtla, 1000 ft,* 3 (TCWC); *1 mi N San Andrés Tuxtla,* 8 (TCWC); *Cueva Laguna Encantada, 3 km ENE San Andrés Tuxtla, 1000 ft,* 1 (TCWC). *Yucatán:* Gruta de Balenkanche, 5 km E Chichén Itzá, 9 (KU). BRITISH HONDURAS. Augustine, 1 (ROM); Rockstone Pond, 2 (ROM). GUATEMALA. *Alta Verapaz:* Río San Simon, 6 km NE Raxruja, 140 m, 2 (TCWC); Lanquin Cave, 1022 ft, 4 (KU); *1 mi W Lanquin, 2000 ft,* 1 (TCWC); 3 km ENE San Cristóbal Verapaz, 1370 m, 22 (TCWC). *Chimaltenango:* Río Queleya, 0.5 mi E Yepocapa, 4300 ft, 4 (KU); *1 m S, 0.75 mi E Yepocapa, 4230 ft,* 41 (KU). *Chiquimula:* Jocotán, near Chiquimula, 1350 ft, 1 (KU). *Escuintla: San Luis, Escuintla,* 2 (UMMZ). *Huehuetenango:* La Democracia, 3300 ft, 8 (TCWC). *Isabal:* 22 km SSW Puerto Barrios, 200 ft, 11 (TCWC); Quebradas, 1000 ft, 8 (FMNH); Puente Punta Gordo, km 51 on Guat. City-Puerto Barrios Hwy., 2050 ft, 3 (KU). *Jutiapa:* Finca el Carnero, Jutiapa, 8 (UMMZ). *Petén:* Toocog, 15 km SW La Libertad, 540 ft, 2 (KU); 12 km NNW Chinajá, 5 (KU). HONDURAS. *Atlantida:* 7 mi E La Ceiba, 100 ft, Atlantida, 3 (TCWC); Balfate, 2 (FMNH). *Comayagua:* Comayagua, 580 m, 3 (TCWC); *3 km W Comayagua, 580 m,* 4 (TCWC); *1 km W Comayagua, 580 m,* 1 (TCWC); *17 km S Comayagua, 580 m,* 1 (TCWC). *Copán:* 6 km ESE Copán, 900 m, 7 (TCWC). *Cortés:* 8 mi SW San Pedro Sula, 500 ft, 2 (TCWC). *Intibucá:* 5 km NE Jesús de Otoro, 640 m, 1 (TCWC). *Lempira:* Las Flores, approx. 10 km N Gracias, 1850 m, 32 (AMNH). *Ocotepeque:* Nueva Ocotepeque, 3 (TCWC). *Santa Barbara:* 2 km S San Nicolás, 600 m, 7 (TCWC). EL SALVADOR. *Cuscatlán:* 2 km W Suchitoto, 390 m, 2 (TCWC). *La Libertad:* 20 km W La Libertad, 250 m, 2 (TCWC); *16.8 km W La Libertad, 30 m,* 1 (TCWC); *13.1 km W La Libertad, 15 m,* 1 (TCWC); *3.5 km E La Libertad, 15 m,* 1 (TCWC); *5.7 km E La Libertad, 15 m,* 14 (TCWC). *La Unión:* Tabanco, 650 ft, 3 (MVZ). *Morazan:* Gigante Mine, approx. 6 mi NE Divisadero, 3 (MVZ); *2 mi N Divisadero,* 1 (MVZ); *Graveyard Mine, 1.5 mi NW Divisadero, 600 ft,* 3 (MVZ); *Encuentros Mine, 3 mi W Divisadero, 700 ft,* 16 (MVZ); *Monte Cristo Mine, 1.5 mi W Divisadero, 750 ft,* 2 (MVZ); *San José Mine, approx. 1 mi W Divisadero,* 1 (MVZ); *Misericordia Mine,* 1 (MVZ). *San Miguel:* Comacaran, 700 ft, 2 (MVZ). NICARAGUA. *Chinandega:* 6.5 km N, 1 km E Cosigüina, 10 m, 1 (KU). *Estelí:* 2 km S Estelí, 3300 ft, 3 (TCWC); *50 mi N Sébaco,* 1 (AMNH). *Matagalpa:* 2 mi SE Darío, 1500 ft, 4 (TCWC). *Río San Juan:* 1 km S El Castillo, 130 m, 1 (TCWC). COSTA RICA. *Guanacaste:* 9 km N Liberia, 4 km E Pan American Highway, 12 (LACM); Río Te-

noria, 3 mi S, 10 mi W Las Cañas, 10 ft, 3 (TCWC). *Puntarenas:* 9 mi ENE Puerto Golfito, 100 ft, 1 (TCWC). PANAMA. *Chiriquí:* Cuesta de Piedra, 3000 ft, 1 (USNM); *1 mi E Cuesta de Piedra, 2800 ft,* 2 (USNM); Guabala, 50 ft, 2 (USNM). *Coclé:* Penonomé, 45 (9 USNM, 36 UMMZ). *Los Santos:* Cerro Hoya, 14 (USNM); *Guánico,* 6 (USNM). *Veraguas:* Isla de Cébaco, 1 (USNM).

Pteronotus parnellii rubiginosus (Wagner)

Chilonycteris rubiginosus Wagner, 1843, Wiegmann's Archiv für Naturgesch., 9:367, 31 December (International Rules of Zoological Nomenclature, Art. 21b, ii, p. 19).

Holotype.—Adult male, skin, skull not removed, Zoologisches Staats-Sammulung, München, West Germany no. 45; from Caicara, Mato Grosso, Brasil; obtained by Johann Natterer on 19 August 1828; original no. 115.

Distribution.—Central America, from central Honduras southward along the humid Caribbean versant through Nicaragua, Costa Rica, and Panamá into South America (Amazonian lowlands to as far south as the Mato Grosso region of Brasil, Tingo María, Perú, and east to Surinam); also on Trinidad. The range of this subspecies is not well-defined in eastern Panamá or in northwestern and eastern Colombia (Fig. 22).

Description.—Size, largest for the species *P. parnellii,* both cranially and externally. Standard external measurements (average, with extremes in parentheses) for 12 males and four females, respectively, from Río Cunucunuma, Belén, 150 m, Amazonas, Venezuela, are as follows: total length, 95.4 (88.0-102.0), 91.2 (87.0-95.0); length of tail vertebrae, 26.2 (23.0-28.0), 25.5 (24.0-27.0); length of hind foot, 16.3 (15.0-17.0), 16.2 (24.0-27.0); length of ear from notch, 25.2 (24.0-28.0), 25.5 (25.0-26.0). Length of forearm for the holotype (measured by Dilford C. Carter) and a female from 264 km N (by road) Xavantina, Mato Grosso, Brasil, are 64.2 and 61.8, respectively; see table 1, for additional external and cranial measurements of representative populations of this subspecies. Members of this subspecies are the darkest in color of all subspecies of *P. parnellii.* Dorsally, fresh pelage is extremely dark brown (near Clove Brown). An August-taken female in fresh pelage, from Santa Rosa, 17 km N and 15 km E Boaco, Nicaragua, was Fuscous Black dorsally. The overall darker appearance of *rubiginosus* can be attributed to the complete obliteration of the central zone of pale coloration on the hairs of the back. This zone, if at all discernible, is only slightly paler in color than the terminal zones. Ventrally, bats of this subspecies are darker, owing to a more extensive Bister-colored basal band on the hairs, which have brownish-white tips. The increased pigmentation of the hairs may account for the brilliant cinnamon color of old pelage, which usually is a rich Ochraceous Orange in other geographic races.

Comparisons.—For comparison with *P. p. mesoamericanus,* see account of that subspecies. From *P. p. fuscus,* the subspecies *rubiginosus* may be distinguished by its larger external and cranial size (Table 1) and darker pelage.

Remarks.—This subspecies occurs from the northern part of the Amazon Basin northward in the east to Trinidad and Surinam, and northward in the west to Central America, where, as was mentioned in the previous account, *rubiginosus* occurs in the Caribbean versant and seems to interbreed freely along a north-south line (roughly coincident with the continental divide) with *P. p. mesoamericanus.*

Koopman (1955:112) indicated that *P. p. fuscus* probably was a synonym of *rubiginosus.* However, after examining a considerable number of specimens from Middle and South America, particularly Venezuela (referable to *rubiginosus*), I conclude that the trinomen *fuscus* is valid and should be retained for the populations of *P. parnellii* from along the Caribbean coast of northern South America (excluding Trinidad).

The resemblance between *rubiginosus* and *fuscus* increases (lower distance coefficients, Fig. 21) in the region of northeastern Venezuela. Physical and ecological barriers posed by an eastern extension of the Andes and the Venezuelan llanos (an extensive east-west grassland area that extends from southeastern Colombia, north of the Río Orinoco, and eastward to the Delta Amacuro), probably separate *fuscus* and *rubiginosus* in northwestern South America. Limited gene flow between these two subspecies probably occurs in eastern Venezuela where the major route for genetic exchange may be through the more mesic Delta Amacuro. The populations of *rubiginosus* on Trinidad with those of the Amazon Basin are probably continuous through the delta region of eastern Venezuela.

In figure 21, it will be noted that localities 55 and 56 are linked by a low distance coefficient and that localities 57, 58, 59, and to a lesser extent 54, likewise are connected by low coefficients. However, these two groups of localities are separated from each other by slightly higher values. These differences are interesting because localities 55 and 56 are situated near the southern edge of the Venezuelan llanos where the tropical forest is not well developed. Localities 57, 58, 59, and 54 are, however, situated in areas of higher humidity and rainfall where the tropical forest is more extensive. In the material examined in this study, specimens of *rubiginosus* were found to be largest in southern Venezuela and Guyana. Unfortunately, insufficient material exists to fully characterize the geographic variation in the Brasilian portion of the Amazon Basin.

Specimens examined (526).—HONDURAS. *Olancho:* San José, Río Tinto, 340 m, 3 (TCWC); *NE Catacamas, 500 m,* 14 (TCWC). NICARAGUA. *Boaco:* Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 1 (KU); Los Cocos, 14 km S Boaco, 220 m, 1 (KU). *Chontales:* No specific locality, 1 (KU). *Zelaya:* Bonanza, 850 ft, 1 (KU); Cara de Mono, 50 m, 4 (KU); *El Recreo,* 1 (LACM); *S side Río Mico, El Recreo, 25 m,* 1 (KU); *Río Mico,* 6 (UMMZ); *10 km W Rama, 40 m,* 12 (TCWC); *2 mi ESE Rama, 200 ft,* 7 (TCWC). COSTA RICO. *Cartago:* 3 km S Moravia, 1 (UMMZ). PANAMA. *Bocas del Toro:* Almirante, 27 (USNM); 7 *km SSE Changuinola,* 1 (USNM). *Canal Zone:* Río Pequeni, Salamanca Hydrographic Station, 7 (MCZ); 3 mi from Cristóbal, 2 (FMNH); Bas Obispo, 12 (USNM); *Sardinilla Mine no. 1, 3 mi E Camboa,* 5 (MVZ); *Barro Colorado,* 4 (UMMZ); *Paraíso,* 53 (USNM); *Summit,* 12 (USNM). *Colón: Buena Vista,* 12 (USNM). *Darién:* El Real, 1 (USNM); *Río Chucunaque,* 2 (USNM). *Panamá: Cerro Azul,* 16 (USNM); *Río Chilibrillo, Bat Caves South of Alhapuila,* 1 (USNM); *Chilibri River,* 7 (USNM). *San Blas:* Head of Río Pito, Armila, 2 (USNM). VENEZUELA. *Apure:* Hato Cariben (La Villa), 60 km NE Pto. Páez, 76 m, 5 (USNM); *Cerro de Murciélago, 8 km NW Pto. Páez, 76 m,* 6 (USNM). *Bolívar:* Ciudad Bolívar, 1 (MLS); Perú Mine, El Callao, 16 (1 FMNH, 2 USNM, 13 AMNH); Hato Florida, 14 km S, 45 km E Caicara, 50 m, 17 (USNM); Maripa, 1 (KU); Los Patos, 28 km SE El Manteco, 3 (USNM); *Río Supamo, 56 km SE El Manteco,* 3 (USNM); Hato San José, 146 km S, 7 km E Ciudad Bolívar, 306 m, 4 (USNM); *Boca de Parguaza al Orinoco,* 3 (IZT); *Isla Orupe, Río Orinoco (Cerca Pto. Páez),* 1 (IZT); El Manaca, 59 km SE El Dorado, 6 (USNM); 10 km NE Icabarú, 1 (USNM). *Territorio Amazonas:* Chaparito, 9 km SE Puerto Ayacucho, 119 m, 1 (USNM); *Raya, 32 km SSE Puerto Ayacucho, 135 m,* 5 (USNM); Río Manapiare, San Juan, 155 m, 17 (USNM); Río Cunucunuma, Belén, 150 m, 17 (USNM); *Tamatama, Río Orinoco, 135 m,* 3 (USNM); Boca Mavaca, 68 km SE Esmeralda, 138 m, 7 (USNM); Río Mavaca, 108 km SE Esmeralda, 140 m, 22 (USNM). GUYANA. [localities not mapped]: *Kanashen, upper Essequibo Wai-Wai village,* 1 (ROM); *Kuitaro River, Rupununi Dist.,* 1 (ROM); *Nappi Creek, Kanuku Mts.,* 1 (ROM). BRASIL. Rio Bronco, Rio Negro, Serra de Cucuhy, 64 (AMNH); [localities not mapped] *Taparinha (on the Amazon River),* 1 (MPEG); *264 km N (by road) Xavantina (12° 51′ S, 51° 46′ W Serra do Roncador), approx. 1750 ft, Mato Grosso,* 1 (USNM). PERU [localities not mapped]. *Tingo María,* 1 (MCZ); *3 mi S Tingo María, 2000 ft, Huánuco,* 38 (TCWC). TRINIDAD. Port of Spain, 2 (USNM); *Zacaya Cave, Montevideo,* 11 (USNM); *Guácharo Cave,* 4 (MCZ); *Oropouche Heights,* 8 (FMNH); *Guanapo Heights,* 17 (1 AMNH, 4 LACM, 12 USNM); *Las Cuevas,* 1 (AMNH); Mt. Tamana Caves, 18 (2 TCWC, 4 ROM, 12 USNM); *Tamana Hill,* 1 (AMNH).

Additional marginal record.—SURINAM.

Tafelberg, Anton van Aerde Cave (Husson, 1962:74).

Pteronotus parnellii fuscus (J. A. Allen)

Chilonycteris rubiginosa fusca J. A. Allen, 1911, Bull. Amer. Mus. Nat. Hist., 30:262, 2 December.

Holotype.—Adult male, skin and skull, AMNH 31561; from Las Quiguas, 5 mi S Puerto Cabello, 650 ft, Venezuela; obtained by M. A. Carriker on 7 September 1910.

Distribution.—Northern South America, along the semiarid Caribbean coast of Colombia and Venezuela (Fig. 22).

Description.—Size, medium for species and similar to that of *P. p. mesoamericanus.* Standard external measurements (average, with extremes in parentheses) for seven males and seven females, respectively, from the vicinity of Urama, Yaracuy, Venezuela, are as follows: total length, 95.3 (93.0-98.9), 87.5 (83.0-94.0); length of tail vertebrae, 24.6 (20.0-27.0), 24.1 (22.0-26.0); length of hind foot, 14.9 (14.0-16.0), 14.7 (13.0-16.0); length of ear from notch, 22.1 (18.0-25.0), 23.1 (23.0-24.0). Additional selected external and cranial measurements are given in table 1.

Fresh pelage of *fuscus,* as the name implies, is dark grayish-brown dorsally. Two February-taken females from 1.5 km S Cariaco, Sucre, Venezuela, are nearly Clove Brown dorsally. Individual hairs from the back of bats from this region are blackish-brown basally and tipped with a zone of Prout's Brown; the central zone is almost indistinguishable from the base, being only slightly paler in color. Ventrally, the pectoral and abdominal regions are dark brown, owing primarily to the dark brown basal bands on the hairs. Each hair has a whitish or buffy tip. Bats of this subspecies on Margarita Island, Nueva Esparta, Venezuela, are somewhat paler (Sayal Brown) in color than adjacent mainland populations.

Comparisons.—For comparison with *P. p. rubiginosus,* see account of that subspecies.

Remarks.—The subspecific name *fuscus* has been variously applied to the Middle American individuals of *P. parnellii* herein designated *mesoamericanus* (Hershkovitz, 1951; Koopman, 1955; Felten, 1956; Hall and Kelson, 1959; Jones, 1966, Jones, *et al.,* 1971; and others).

The variation within this subspecies is similar to that discussed in each of the above accounts, that is, geographic departure from the typical population results in a certain degree of phenotypic deviation. In this case, the trend is generally toward larger size either to the westward or eastward from northwestern Venezuela. To the west, *fuscus* may intergrade with *rubiginosus* and perhaps *mesoamericanus* in eastern Panamá and northwestern Colombia as discussed previously. To the east, due to an apparent breakdown of the mountain and grassland barriers that apparently partially isolate coastal populations of *fuscus,* there seems to be limited gene exchange with *rubiginosus.*

Of interest in northeastern Venezuela is a notable reduction in overall size of specimens of *fuscus* from Margarita Island (Table 1, locality 52). Bats from there were netted on the northeastern end of the island where the habitat is somewhat mesic and on the western end where conditions are extremely xeric. The point to be made here is that, again, in an area where less than optimal habitat prevails, *P. parnellii* deviate phenotypically from the typical population.

The close resemblance between *fuscus* and the Middle American subspecies herein designated *mesoamericanus* is one of the most interesting problems encountered during this study. Previously bats of these two subspecies were assigned to *fuscus* by various authors. This assignment evidently resulted from a paucity of material formerly available from the region of Guatemala south to northern South America. Climatic and ecological fluctuations in eastern Panamá and northwestern Colombia during

the Pleistocene seem to have been key factors in the evolution of these two races; the continued maintenance of this resemblance may relate to similarity in the habitats occupied by each.

Typically, *fuscus* averages slightly larger than *mesoamericanus* (Fig. 19), although there is broad overlap. The differences are such that if the two populations were contiguous I would not have proposed recognition for *mesoamericanus*. However, in view of the fact that both *fuscus* and *mesoamericanus* enter into a zone of intergradation with *rubiginosus*, in eastern Panamá and adjacent regions of Colombia, and diverge from this zone as distinct units, indicates a certain degree of independence, possibly including independent adaptation to a similar environment. I therefore propose that they be recognized as separate subspecies to better represent the observed geographic variation.

Specimens examined (221).—COLOMBIA. *Bolívar:* Cartagena, 1 (ROM); Coloso, Las Campanas, 250 m, 16 (FMNH); Norosí, Mompas, 1 (USNM); *Magdelena:* Colonia Agrícola de Caracalicito, Santa Marta, 400 m, 4 (USNM). VENEZUELA. *Aragua: Rancho Grande, 1100 m,* 24 (1 UMMZ, 4 MLS, 6 USNM, 13 IZT). *Carabobo: Río Yaracuy, 10 km NW Urama, 25 m,* 4 (USNM); *6 km NW Urama, 60 m,* 3 (USNM); San Esteban, 12 (2 USNM, 10 AMNH); *Las Quiguas, 5 mi S Puerto Cabello, 650 ft,* 6 (1 FMNH, 5 AMNH). *Distrito Federal:* El Limón, 3 km S, 46 km W Caracas, 398 m, 2 (USNM); *Trapiche (Cerca de El Limón),* 1 (IZT). *Guárico: 57 km S, 49 km E Caracas, 630 m,* 3 (USNM); Cueva de Los Murciélagos, Loma de Medio, 460 m, 1 (MLS); *Cueva Loma del Medio, 7 km S San Juan de Los Morros (Carretera a sur de Sebastián),* 3 (IZT). *Miranda:* Los Teques, 1700 m, 1 (IZT); Curapao, 19 km E Caracas, 1160 m, 5 (USNM); *Cueva Walter Dupuy-Capaya,* 1 (MLS); *Cueva Alfredo Jahn, 70 m,* 20 (9 IZT, 11 MLS). *Monagas:* 8 km NW (by road) Caripito, 1 (KU); San Agustín, 2 km N, 3 km W Caripe, 1165 m, 1 (USNM); *Caripe, 900 m,* 20 (IZT); *Cueva del Guácharo, 1050 m,* 1 (MLS). *Nueva Esparta:* Cerro Mata Siete, 2 km N, 2 km E La Asunción, 305 m, 1 (USNM); *La Aguada, 3 km S La Asunción, 53 m,* 12 (USNM); *Cueva Atagua, Cerro Atagua,* 5 (MLS); *Cueva Honda del Piache, SE El Valle,* 2 (RMNH); *El Valle, 50 m,* 2 (KU); *Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m,* 9 (KU). *Sucre:* Caserio Santa Fé, 1 (MLS); *Tacal, 11 km SSW Cumaná,* 2 (KU); *Río Grande, Cerca de Juan Antonio, 10 m,* 1 (MLS); 1.5 km S Cariaco, 3 (KU); 1.5 km NW El Pilar, 1 (KU); Río Salado, 9 km N, 4 km E Güiria, 90 m, 9 (USNM); *Ensenada Cauranta, 7 km N, 5 km E Güiria, 1 m,* 2 (USNM). *Trujillo:* Agua Santa, 23 km NW Valera, 90 m, 2 (USNM). *Yaracuy:* Minas de Aroa, Bolívar R. R., 11 (1 FMNH, 4 MLS, 6 AMNH); 19 km NW Urama, 7 (USNM).

Subgenus **Chilonycteris** Gray

Type species.—Chilonycteris macleayii Gray.

Distribution.—From southern Sonora and Tamaulipas, México, southward (excluding portions of the Mexican Plateau and most of the Yucatan Peninsula) into South America, including Trinidad, to Mato Grosso, Brasil. The subgenus is represented on the Greater Antilles by two endemic species—*Pteronotus fuliginosus* and *P. macleayii*. For additional information concerning distribution, see accounts beyond and figures 24, 27, and 28.

Description.—Size small, forearm usually less than 50; wing membranes attached high on sides of body, leaving a narrow, hair-covered band on back; labio-nasal plate simple to moderately complex, margin above each nostril smooth with irregular, rounded, wart-like tubercles (three to four tubercles over each nostril) or with an elongate, squared excrescence, lateral spikes absent in *P. personatus* but present in both *fuliginosus* and *macleayii* (Fig. 11B, and D-E); tragus relatively simple, spatulate, with a moderately well-developed and shelf-like secondary fold or with prominent secondary fold covered with many long and short hairs (Fig. 10, B-D); antero-medial edge of pinna of ear with two to four, or occasionally as many as six, tooth-like serrations; ears connected by two low, inconspicuous ridges that meet on top of the muzzle and form a prominent rostral tubercle

in *personatus* and a low rostral tubercle in *fuliginosus* and *macleayii*; pelage distinctly tricolored dorsally (more prominent in *fuliginosus* and *macleayii* than in *personatus*); profile of skull relatively flat, although rostrum may be slightly upturned; forehead slopes gradually in *personatus*, but rather abruptly in the Antillean species; braincase ovoid in shape in *personatus* and globular in *fuliginosus* and *macleayii*; rostral breadth almost always less than, or equal to, the length of the maxillary toothrow; upper incisors reduced in size, inner pair bifurcate and with a narrow rounded heel directed laterally toward canine; inner and outer incisors of each premaxillary compressed together, forming two groups with just the inside tips of the inner two incisors touching (this character shared with the subgenus *Pteronotus*); diastema usually present between outer incisors and canine (more prominent in Antillean species); lower incisors reduced in size, all trilobed and with short, rounded heel; tympanic ring large, almost completely covering auditory bulla; basioccipital region broad between bullae, with two large extremely shallow, oval-shaped pits, into which the *M. longus capitus* inserts.

Remarks.—This subgenus and the subgenus *Pteronotus* are similar and probably more closely related than either is to the subgenus *Phyllodia*. Externally *Chilonycteris* is easily distinguished from *Pteronotus* by the absence of a naked back, structure of the tragus, and structure of the labio-nasal plate. Cranially, the two subgenera are similar. They differ, however, in shape and proportions of the braincase and rostral regions; *Pteronotus* being broader in both respects (Figs. 25 and 34).

Pteronotus macleayii (Gray)
MacLeay's Mustached Bat

(Synonymy under subspecies)

Distribution.—Cuba and Jamaica (Fig. 24).

Description.—Size small, forearm usually measuring 40 to 45; wing membrane and uropatagium attached to ankle by way of a long ligament that is tightly bound to the distal half of tibia; tragus long and spatulate, secondary fold prominent, sparsely clothed by short bristle-like hairs, with longer hairs on cranial and distal edges (Fig. 10D); labio-nasal plate distinct, a squared lappet above each nostril and prominent lateral spikes to either side of nostrils (Fig. 11D); one or two (occasionally three) tooth-like serrations on anteromedial edge of pinna; ears connected by an extremely low, inconspicuous ridge that is fused on top of the nose, rostral tubercle not prominent; clitoris unusually long; pelage tricolored dorsally; profile of skull relatively flat, rostrum slightly elevated, forehead rises abruptly onto round, high braincase; rostrum longer than braincase (Fig. 25); marked diastema between outer upper incisor and canine; inner incisors distinctly bifurcate; lower incisors reduced in size and trilobed with short, rounded heels.

Relationships.—This species is most closely related to *P. fuliginosus*, which also inhabits the Greater Antillean region. Both are small species, but may be readily separated by length of forearm as well as condylobasal length, *macleayii* being the larger in both respects. In addition, *macleayii* has a longer and broader rostrum than *fuliginosus* (Fig. 25). Both Antillean species seem to be closely allied to the mainland *P. personatus*, although differ from it in construction of the tragus and labio-nasal plate, and in shape of the braincase. Along with *Mormoops blainvillii*, *P. fuliginosus* and *macleayii* may represent a relatively early invasion of the Greater Antilles by mormoopids as discussed in a later section.

Geographic variation.—The populations of *P. macleayii* from Cuba and Jamaica are currently allocated to the subspecies *macleayii* and *grisea*, respective-

ly. Analysis of geographic variation of this species verifies the distinctness of these two populations in that significant differences were computed between them for every character examined, except breadth across the post-palatal extension. Cuban representatives of the species are consistently smaller in overall size than those from Jamaica.

Remarks.—There has been some confusion in the literature with respect to the identity and distinctness of the species *macleayii* and *fuliginosus*, evidently stemming from mislabeling of the holotypes of the two species. I am grateful to J. Knox Jones, Jr., Karl F. Koopman, and especially John Edwards Hill, who examined the holotypes and contributed to resolution of this confusing problem.

Gray (1839:4) described *Chilonycteris macleayii* based on material from Cuba presented to him by W. S. MacLeay. According to Hill (personal communication), records at the British Museum (a manuscript catalogue prepared by Gray) showed that MacLeay gave Gray three specimens of *Chilonycteris* from Cuba. These appear in the British Museum register under the number BM 38.6.21.8. Gray's (1839:4) description was extensive and delimits accurately the species herein designated *P. macleayii*. Salient points in his description were "edge of the nose with two tooth-like expansions on each side, one over each nostril," and that the length of the forearm was 1.5 inches (approximately 38 mm). The labio-nasal plate illustrated by Gray (1839:pl. 1, fig. 2) agrees exactly with that illustrated in figure 11D. Apparently, the skull was not removed at the time of Gray's description.

Gray's (1843a:20) description of *Chilonycteris fuliginosa* is not nearly so long nor so detailed as that for *macleayii*. Gray noted that *fuliginosa* agreed in many respects with *Chilonycteris macleayii*, but differed from the three specimens of that species in the collection of the British Museum in being darker in color and having larger and rather narrower ears. No mention was made regarding the labio-nasal plate. The holotype of this species bears the register number BM 42.11.24?, and the skull has not been removed from this specimen.

In September of 1968, J. Knox Jones, Jr. compared several specimens of supposed *macleayii* and *fuliginosus* with mormoopid holotypes housed in the British Museum. His conclusions were that the labeled holotypes of both *macleayii* (skull removed) and *fuliginosa* belonged to one and the same species, and agreed completely with a supposed individual of *fuliginosus* from Cuba. In addition, the labio-nasal region of both holotypes agreed with that shown in figure 11E. On the other hand, *Chilonycteris grisea*, as described by Gosse (1851), agreed with a supposed specimen of *macleayii* and figure 11D. These results were indeed perplexing, since Gray (1839) and later Dobson (1878) clearly illustrated the labio-nasal plate that agreed precisely with material currently assigned to *macleayii*. I asked Karl F. Koopman, who visited the British Museum shortly afterward, to re-examine these particular holotypes using his knowledge of the group. His conclusions verified those of Jones. This led me to re-examine all of the descriptions and pertinent literature concerning these holotypes; later I corresponded with J. E. Hill, asking if he could shed some light on this subject. Hill approached this matter by trying to trace the three specimens originally given to Gray. He commented (personal communication), as follows:

"One, a male, is the reputed type specimen. It is also in a bottle labeled comparatively recently by G. W. C. Holt and lacks any identifying mark except a loose label in the bottle, written by R. W. Hayman and bearing only the registration number BM 38.6.21.8. Its identity with the type of *fuliginosa* is

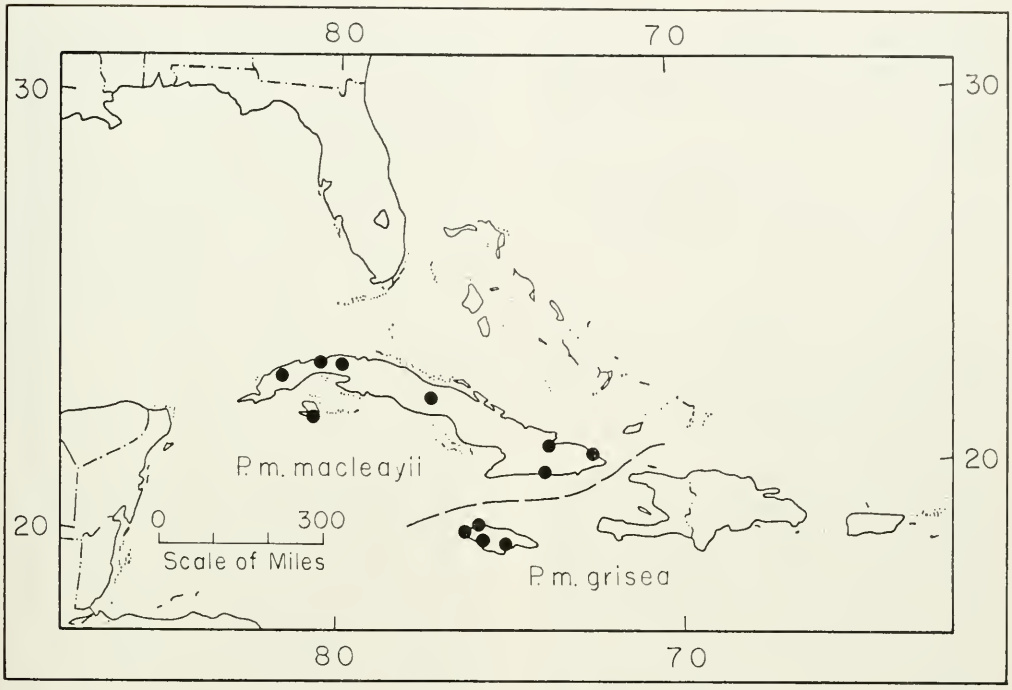


FIGURE 24. Distribution of *Pteronotus macleayii.*

indicated by a remark on the bottle label of the latter by Holt which reads '= *C. macleayi.*'

"The other male example is in a bottle first labeled by Gray and subsequently by Dobson. It is evidently the original container: inexplicably, there is also a specimen of *Pteronotus davyi* in the bottle. Dobson has labeled the bottle 'Type' and '♀ and ♂' but the word type and the symbols have been obliterated at some time. However, the bottle also contains a loose label written by Dobson, which reads '*Chilonycteris macleayi* type.' This male specimen is clearly referable to the species which you characterize as *macleayii.*

"To some extent the female specimen eludes me. However, the collections include a female *Chilonycteris,* BM 7.1.1.700, from the Tomes Collection, its bottle labeled by Gray as *Chilonycteris macleayi,* from Macleay. An addition to the register entry for this specimen reads 'No doubt typical: Apparently from Brit. Mus.' It seems to me that this may be the female listed by Gray and Dobson and that it found its way into the collection of R. F. Tomes, returning here when that collection was accessed in 1907. The specimen agrees with the type of *fuliginosa.*"

At the beginning of World War II, type specimens were segregated from the general collections at the British Museum. Hill is of the opinion that probably the two males described above were in the same bottle and that the wrong specimen later was segregated as the holotype. This error may then have been compounded by subsequent labeling. Hill also wrote that the specimens may have been incorrectly segregated by either Thomas or Dobson.

The solution to this problem suggested by Hill, and one that is acceptable to me, is to take the second male as the holotype of *Chilonycteris macleayii.* Gray apparently had two kinds of mormoopid bats in the MacLeay accession

—a large species and a smaller one. Gray's (1839) description and illustration of *Chilonycteris macleayii* clearly refer to the larger bat here designated *Pteronotus macleayii*.

Pteronotus macleayii macleayii (Gray)

Chilonycteris macleayii Gray, 1839, Ann. Nat. Hist., 4:5, September.

Holotype.—Adult male, preserved in alcohol, skull apparently not removed, BM 38.6.21.8; from Cuba; collected by W. S. MacLeay. See remarks in species account of *P. macleayii* above.

Distribution.—Cuba (Fig. 24).

Description.—Smaller of the two subspecies of the species, both cranially and externally. Most specimens examined were preserved in alcohol, thereby making difficult an accurate assessment of color. A December-taken male, from Soledad, Las Villas, Cuba, has relatively fresh pelage that is tricolored dorsally. Individual hairs from the back have olive-brown basal bands and dark brown to blackish brown tips. The central band is whitish to grayish white. The head does not differ appreciably in color from the back. Ventrally, the pelage is grayish white with a pale buffy tinge. The hairs from the pectoral and abdominal regions are sharply bicolored, being Clove Brown at the base and tipped with grayish white; on the throat and chin, hairs are more nearly monocolored or have pale Snuff Brown bases. Of three individuals, from San Vicente, Pinar del Río, captured on 26 July, one, a male, resembles the specimen described above, being only slightly darker. The other two specimens are females that are Ochraceous Orange in color.

Measurements.—Selected external and cranial measurements (average, with extremes in parentheses, plus or minus two standard errors of the mean) of 15 adult males from Cuba, are as follows: length of forearm (12 specimens only), 42.1 (41.2-43.4) ± 0.37; zygomatic breadth, 7.8 (7.6-8.0) ± 0.07; rostral breadth, 6.1 (5.9-6.5) ± 0.09; length of maxillary toothrow, 6.6 (6.4-6.8) ± 0.05; condylobasal length, 14.5 (14.1-15.0) ± 0.15; depth of cranium, 6.9 (6.4-7.1) ± 0.09.

Standard external measurements (average, with extremes in parentheses) of four males from Baracoa, Oriente, Cuba, are as follows: total length, 62.7 (61.0-65.0); length of tail vertebrae, 21.7 (20.0-23.0); length of hind foot, 13.7 (12.0-15.0); length of ear from notch, 9 for each individual.

Comparisons.—From *P. m. grisea* of Jamaica, *P. m. macleayii* may be distinguished on the basis of smaller external and cranial size (see measurements). In addition, the cranium of *macleayii* is noticeably narrower and shorter than that of *grisea* (Fig. 25). These two subspecies do not appear to differ in color, although additional material will be necessary before this can be precisely judged.

Remarks.—In the past, some authors have placed the name *Lobostoma quadridens* Gundlach, 1840, in synonymy under *P. m. macleayii*. Close examination of Gundlach's description indicates that specimens of both the species *macleayii* and *fuliginosus* probably were present in his sample; no holotype or type series was designated. I therefore, regard Gundlach's *quadridens* as a *nomen dubium*.

Specimens examined (82).—CUBA. *Habana:* Cueva de Mudo, Güines, 6 (ROM); *Bucuranao*, 1 (AMNH). *Oriente:* Cueva Zuntiaga, Barajagua-Mayarí, 2 (MCZ); Baracoa, 44 (2 FMNH, 10 MCZ, 32 USNM); *Cueva de Majana, Baracoa*, 11 (4 AMNH, 7 MCZ); Santiago, 1 (USNM). *Pinar del Río:* Cueva del Río, San Vicente, 1 (TCWC); *San Vicente*, 12 (11 AMNH, 1 LACM); *Banos San Vicente*, 2 (USNM). *Las Villas:* Soledad, Harvard Botanical Gardens, 1 (ASC). *Isla de Pinos:* Cueva de Pedernales, south coast, 1 (AMNH).

Pteronotus macleayii grisea (Gosse)

Chilonycteris grisea Gosse, 1851, A naturalist's sojourn in Jamaica. Mem. Council Royal Soc. Agric., Jamaica, p. 326.

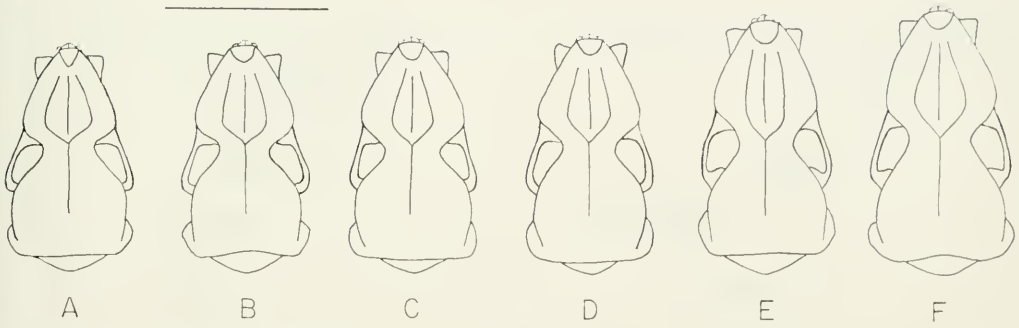


FIGURE 25. Dorsal view of skulls of *Pteronotus fuliginosus torrei* (A, Cuba), *P. f. fuliginosus* (B, Jamaica; C, Dominican Republic; D, Puerto Rico), *P. m. macleayii* (E, Cuba), and *P. m. grisea* (F, Jamaica). All specimens are adult males; horizontal line above B is 10 mm in length.

Holotype.—Adult male, preserved in alcohol, skull not removed, BM (no registration number); from Phoenix Park, near Savanna la Mar, Westmoreland Parish, Jamaica.

Distribution.—Jamaica (Fig. 24).

Description.—Size large for the species. Eight January-taken specimens from Oxford Cave, Balaclava, Jamaica, are in relatively fresh pelage which is dark brown dorsally. The basal and terminal color bands of hairs on the back are dark brown (Bister Brown to Prout's Brown); the central color band is grayish white. Ventrally, the pectoral and abdominal regions are grayish white tinged with buff, the throat and chin being somewhat paler.

Measurements.—Selected external and cranial measurements (average, with extremes in parentheses, plus or minus two standard errors of the mean) of 19 adult males (sample size in brackets if different) from Jamaica are as follows: length of forearm, 43.5 (41.7-45.1) ± 0.33 [33]; zygomatic breadth, 8.2 (8.0-8.4) ± 0.05; rostral breadth, 6.4 (6.3-6.6) ± 0.04; length of maxillary toothrow, 6.8 (6.7-7.0) ± 0.03; condylobasal length, 15.2 (14.8-15.7) ± 0.10 [17]; depth of cranium, 7.1 (6.9-7.3) ± 0.06.

Standard external measurements (average, with extremes in parentheses) of six males and six females from Providence Cave, Montego Bay, Jamaica, are as follows: total length, 74.2 (73.0-75.0), 74.3 (72.0-78.0); length of tail vertebrae, 23.7 (22.0-25.0), 23.3 (22.0-25.0); length of hind foot, 9.4 (9.0-10.0), 9.9 (9.5-10.0).

Comparisons.—For comparison with *P. m. macleayii,* see account of that subspecies.

Remarks.—The degree of difference between the Jamaican subspecies, *grisea,* and *macleayii* from Cuba seems to indicate the relative effectiveness of the water barrier between the two islands. In view of their small size, which may greatly affect their ability to cross the strait between the two islands, it is doubtful that any substantial gene flow now exists between these two races.

Specimens examined (69).—JAMAICA. *Hanover:* Lucea, 4 (AMNH). *St. Catherine:* St. Clair Cave, 12 (3 LACM, 9 USNM); *Spanish Town,* 1 (USNM). *St. Elizabeth:* Oxford Cave, Balaclava, 8 (AMNH). *St. James:* Providence Cave, Montego Bay, 22 (AMNH); *Montego Bay,* 22 (USNM).

Pteronotus fuliginosus (Gray)
SOOTY MUSTACHED BAT

(Synonymy under subspecies)

Distribution.—Cuba, Jamaica, Hispaniola, and Puerto Rico (Fig. 27).

Description.—Size small, forearm usually less than 40.0; wing membrane and uropatagium attached to ankle by way of a long ligament that is tightly bound to the distal half of the tibia;

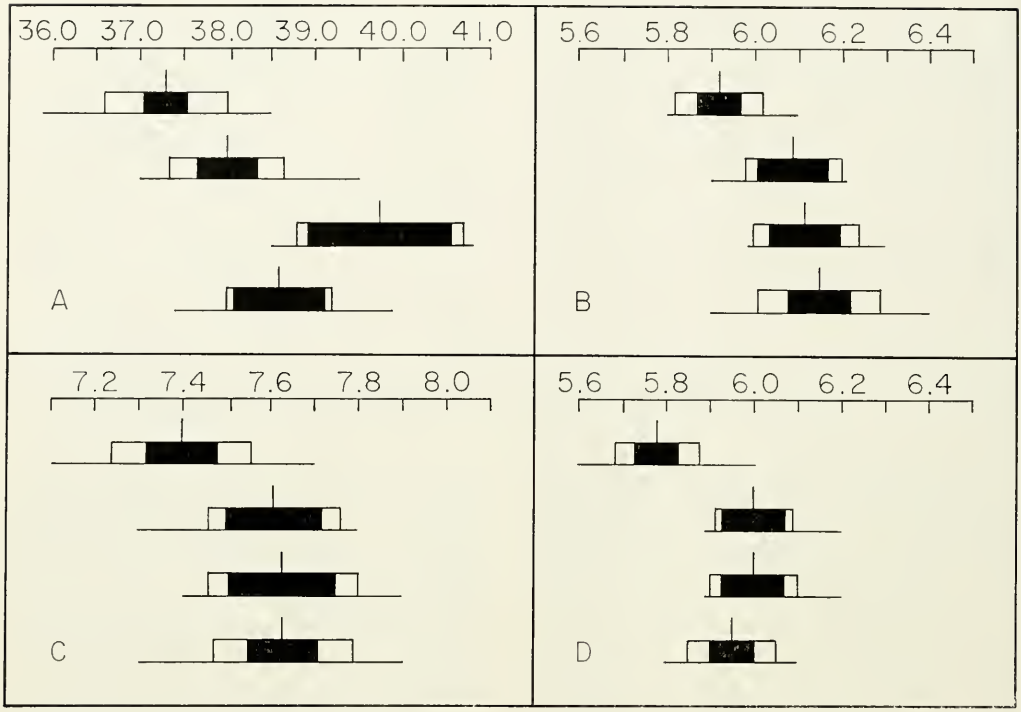


FIGURE 26. Dice-squares illustrating geographic variation of *Pteronotus fuliginosus* from the Greater Antillean islands of Cuba, Jamaica, Hispaniola, and Puerto Rico (top to bottom). The measurements illustrated (in mm) are: A, length of forearm; B, rostral breadth; C, zygomatic breadth; D, length of maxillary toothrow. The thin horizontal line represents the range of variation and the thin vertical line the mean; the blackened part of the horizontal bar equals two standard errors on either side of the mean and the white part indicates one standard deviation on either side of the mean. See text for discussion.

tragus long and spatulate, secondary fold prominent, sparsely covered with short bristle-like hairs, with longer hairs on cranial and distal edges (Fig. 10C); labio-nasal plate moderately complex, margin above each nostril with three to four wart-like tubercles, nostrils separated by slight emargination, prominent lateral spike on either side of nostrils (Fig. 11E); three to four tooth-like serrations on antero-medial edge of long, lanceolate portion of the ear; ears connected by two extremely low, inconspicuous ridges that fuse on top of nose, rostral tubercle not prominent; pelage distinctly tricolored dorsally, hairs of back having three well-marked bands, pelage bicolored ventrally; profile of skull relatively flat, rostrum slightly elevated, forehead rises abruptly onto round, high braincase; rostrum approximately same length as braincase (not noticeably longer—Fig. 25); marked diastema between outer upper incisor and canine; inner incisors distinctly bifurcate; lower incisors reduced in size and trilobed with short, rounded heels.

Relationships.—See discussion of relationships in foregoing account of *Pteronotus macleayii.*

Geographic variation.—As currently understood, the representatives of this species from Jamaica and Hispaniola are assigned to the subspecies *fuliginosus* and those from Puerto Rico to *inflata*; bats from Cuba have been referred to a distinct species, *torrei.* My analysis of geographic variation, indicates that the populations of *P. fuliginosus* from Jamaica, Hispaniola, and

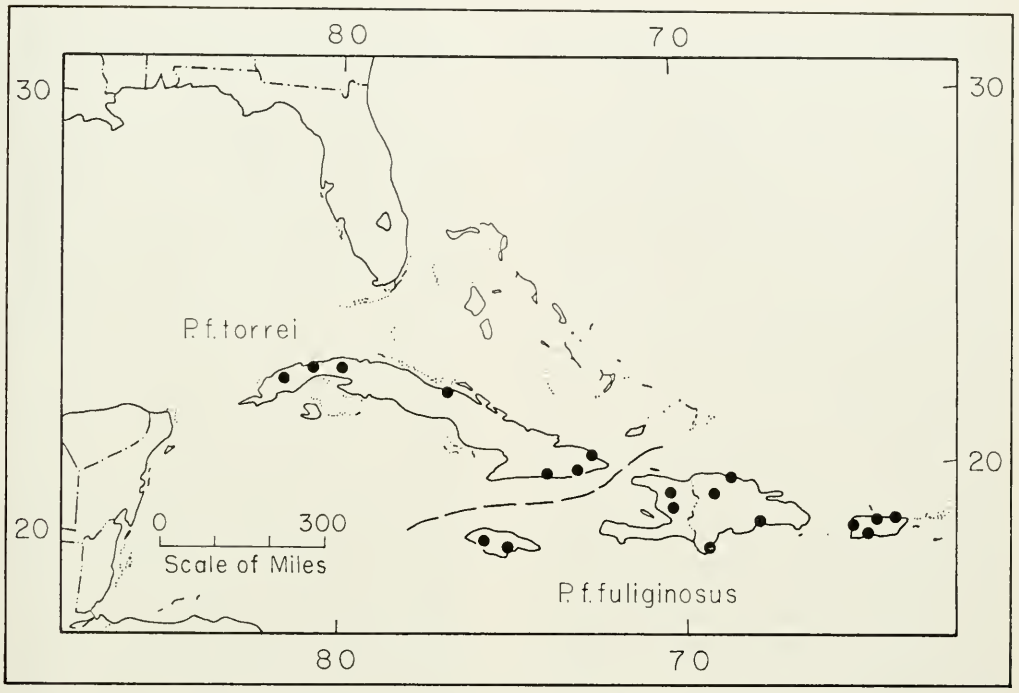


FIGURE 27. Distribution of *Pteronotus fuliginosus.*

Puerto Rico are more or less homogeneous. On the other hand, these populations are separated by non-overlapping subsets of means from Cuban bats. The only characteristic in which non-overlapping subsets of means was not observed was the length of the forearm. In external and cranial size, the Cuban bats are smaller than bats from the other Greater Antillean islands (Figs. 25-26). Generally, the largest representatives of this species are from Hispaniola and Puerto Rico. The bats of the Jamaican population are intermediate in size between those of Cuba and Hispaniola and Puerto Rico. Therefore, it seems that only two populations merit recognition at the subspecific level.

Pteronotus fuliginosus fuliginosus (Gray)

Chilonycteris fuliginosa Gray, 1843, Proc. Zool. Soc. London, p. 20, 28 February.

Chilonycteris macleayii inflata Rehn, 1904, Proc. Acad. Nat. Sci. Philadelphia, 56:190, 26 March. Type locality, Cueva di Fari, near Pueblo Viejo, Puerto Rico. Holotype, adult male, preserved in alcohol, skull removed, ANSP 6234; obtained on 19 March 1900, by Dr. C. W. Richmond and Dr. L. Steneger.

Holotype.—Adult male, preserved in alcohol, skull not removed, BM 42.11. 24? (registration number currently in doubt); from Port au Prince, Haiti; presented by J. N. Tweedy.

Distribution.—Greater Antillean islands of Jamaica, Hispaniola, and Puerto Rico (Fig. 27).

Description.—Size large for the species. The pelage of these bats is distinctly tricolored dorsally. However, the majority of specimens of this species that I examined were preserved in alcohol, making accurate color descriptions difficult. A series of males and females from Montego Bay, captured on 31 December, were in relatively fresh pelage. Dorsally, specimens were grayish brown. Hairs of the back have three distinct color bands, the broadest of these being a central band that is grayish white to buffy white; the basal and terminal

bands are dark brown or Fuscous Black. Ventrally, the overall color is grayish white in the pectoral and abdominal regions; the individual hairs are bicolored with Clove Brown basal bands and terminal bands that are whitish or grayish white. The throat and chin are slightly paler than other parts of the venter owing to a reduction of the dark basal portion of the hairs. An adult male from the Dominican Republic, captured on 17 October, is in fresh pelage that is extremely dark brown, almost black in color.

Measurements.—Selected external and cranial measurements (average with extremes in parentheses, plus or minus two standard errors of the mean) of eight adult males from Jamaica, nine from Hispaniola, and 18 from Puerto Rico (sample size in brackets if different) respectively, are as follows: length of forearm, 38.0 (37.0-39.5) ± 0.34 [16], 39.8 (38.5-40.8) ± 0.83 [5], 38.3 (30.1-39.9) ± 0.59 [31]; zygomatic breadth, 7.6 (7.3-7.8) ± 0.11, 7.6 (7.4-7.9) ± 0.12, 7.6 (7.3-7.9) ± 0.08; rostral breadth, 6.1 (5.9-6.2) ± 0.08, 6.1 (6.0-6.3) ± 0.08, 6.1 (5.9-6.4) ± 0.07; length of maxillary toothrow, 6.0 (5.9-6.2) ± 0.07, 6.0 (5.9-6.2) ± 0.07, 6.0 (5.8-6.1) ± 0.05 [19]; condylobasal length, 13.5 (13.2-13.8) ± 0.15 [7], 13.6 (13.3-14.1) ± 0.15, 13.6 (13.2-13.9) ± 0.10 [17]; depth of cranium, 6.8 (6.7-7.1) ± 0.10, 7.1 (6.7-7.3) ± 0.13, 7.1 (6.9-7.7) ± 0.09 [17].

Standard external measurements (average, with extremes in parentheses) of 13 males and 13 females, respectively, from St. Clair Cave, St. Catherine Parish, Jamaica, are as follows: total length, 60.2 (58.0-64.0), 61.1 (59.0-66.0); length of tail vertebrae, 18.8 (16.0-21.0), 19.3 (18.0-22.0); length of hind foot, 8.8 (8.0-10.0), 9.0 (8.0-10.0); length of ear from notch, 15.3 (15.0-16.0), 15.2 (14.0-16.0).

Comparisons.—From *P. f. torrei* of Cuba, *P. f. fuliginosus* is readily distinguished on the basis of larger external and cranial size (Figs. 25-26), although there may be slight overlap in the range of any one measurement.

Remarks.—Rehn (1904) distinguished "*Chilonycteris macleayii inflata*" from *fuliginosus* primarily on the basis of a more inflated rostrum in the former. The breadth of the rostrum of the holotype (ANSP 6234) is 6.4, which falls at the upper end of variation observed in populations of *P. fuliginosus*. However, in view of the other similarities between populations of *P. fuliginosus* from Jamaica, Hispaniola, and Puerto Rico, I regard the subspecies *inflata* as a junior synonym of *P. f. fuliginosus*.

Specimens examined (265).—JAMAICA. *St. Catherine:* St. Clair Cave, 29 (27 ROM, 2 USNM). *St. Elizabeth:* Oxford Cave, Balaclava, 8 (AMNH); Balaclava, 28 (26 AMNH, 2 MCZ). HAITI. San Michel, 2 (USNM); 4 mi SE Cerca La Source, 52 (USNM); no specific locality, 1 (AMNH). DOMINICAN REPUBLIC. *Distrito Nacional:* Caña Honda, Santo Domingo, 1 (AMNH). *Pedernales:* 6 mi NE Oviedo, 1 (ASC). *Puerto Plata:* Sosúa, 2 (1 ASC, 1 MCZ). *Santiago Rodriguez:* Cueva Clavijo, 12 km W Monción, 2 (1 AMNH, 1 FMNH). No specific locality, 4 (ANSP). PUERTO RICO. Cueva di Fari, near Pueblo Viejo, 46 (12 AMNH, 2 ANSP, 9 UMMZ, 23 USNM); *7.5 km E Guaniana,* 1 (ASC); *Cueva de Burro, between Vega Alta and Vega Baja,* 25 (10 UMMZ, 15 USNM); Cueva de Trujillo Alto, 59 (AMNH); *San Juan,* 1 (USNM); Mayaguez, 2 (USNM); Toro Negro Doña Juan Recreation Area, 1 (ROM).

Pteronotus fuliginosus torrei
(G. M. Allen)

Chilonycteris torrei G. M. Allen, 1916, Proc. New England Zool. Club, 6:4, 8 February.

Holotype.—Adult female, preserved in alcohol, skull removed, MCZ 11672; from La Cueva de La Majana, Baracoa, Oriente Province, Cuba; obtained by Sr. Victor José Rodriguez y Verrier, on 15 June 1915.

Distribution.—Cuba (Fig. 27).

Description.—Size small, both externally and cranially, for species (see measurements). In addition to small size, *torrei* has a narrow rostrum that is

noticeably attenuate at the tip; the nasal aperture also is narrow (Fig. 25). The pelage is short and dark brown in color dorsally. The central color band of hairs from the back appears to be somewhat more restricted and more brownish in December-taken specimens of this race compared with individuals of *P. f. fuliginosus* from Jamaica taken at the same time of year. Ventrally, the pelage is pale Snuff Brown or buffy brown.

Measurements.—Selected external and cranial measurements (average with extremes in parentheses, plus or minus two standard errors of the mean) of 15 adult males from Cuba (sample size in brackets, if different) are as follows: length of forearm, 37.3 (35.9-38.5) ± 0.26 [30]; zygomatic breadth, 7.4 (7.1-7.7) ± 0.08; rostral breadth, 5.9 (5.8-6.1) ± 0.05; length of maxillary toothrow, 5.8 (5.6-6.0) ± 0.05; condylobasal length, 13.2 (12.8-13.4) ± 0.09; depth of cranium, 6.7 (6.4-7.2) ± 0.11. No reliable standard external measurements are available.

Comparisons.—For comparison with *P. f. fuliginosus*, see account of that subspecies.

Remarks.—The subspecies *torrei* has been regarded by most authors as a full species since its description by G. M. Allen (1916). However, after corresponding with Oldfield Thomas, Allen (1917:168) noted that *torrei* "should best be considered as a subspecies of *fuliginosa*," a point of view with which I fully agree.

Specimens examined (119).—CUBA. *Habana:* Cueva de Mudo, Güines, 6 (ROM); *Cueva del Infreno, near Tapaste,* 1 (USNM). *Las Villas:* Cueva de Colón, Yaguajay, Punta Caguanes, 2 (AMNH). *Oriente:* Baracoa, 15 (USNM); *8 mi E Baracoa,* 24 (USNM); *Cueva de Majana,* 6 (USNM); San Carlos Estate, Guantanamo, 1 (USNM); Banabacóa, Dos Caminos, 1 (USNM). *Pinar del Río:* Cueva del Río, San Vicente, 9 (7 ASC, 2 TCWC); *Cueva del Indio, San Vicente,* 44 (AMNH); *San Vicente,* 1 (LACM); Guanajay, 9 (USNM).

Pteronotus personatus (Wagner)

Wagner's Mustached Bat

(Synonymy under subspecies)

Distribution.—From southern Sonora and Tamaulipas, México, southward (excluding portions of the Mexican Plateau and most of the Yucatan Peninsula) through Central America (although not yet recorded from British Honduras or Nicaragua) into South America (including Trinidad) as far as the Mato Grosso region of Brasil (Fig. 28). The geographic range of this species in the Amazon Basin is poorly known.

Description.—Size small; uropatagium and wing membranes attach to ankle by way of a short ligament that is tightly bound to tibia; tragus spatulate, secondary fold moderately well developed and shelf-like, clothed with short hairs (Fig. 10B); labio-nasal plate simple, margin above nostrils smooth or with several wart-like tubercles, nostrils not separated by deep emargination, lacking lateral spikes on either side of nostrils (Fig. 11B); anterio-medial edge of pinna with three to four (occasionally as many as six) tooth-like serrations; ears united by two low, inconspicuous ridges that fuse on top of muzzle and form a prominent rostral tubercle; profile of skull relatively flat, rostrum slightly elevated, forehead sloping gradually onto long, oval-shaped braincase; upper incisors reduced, slight diastema between outer incisor and canine; inner incisors distinctly bifurcate, with a narrow, rounded heel; lower incisors reduced and having short rounded heel, inner pair distinctly trilobed, outer pair weakly trilobed; small, shelf-like cuspule on anterior lingual surface of postcentrocrista (terminology of Van Valen, 1966:9) on M1 and M2 (this cuspule, found in no other mormoopid, is in a position that roughly approximates that of the metaconule); infraorbital foramen opening just slightly anterior to maxillary root of zygomatic arch, canal

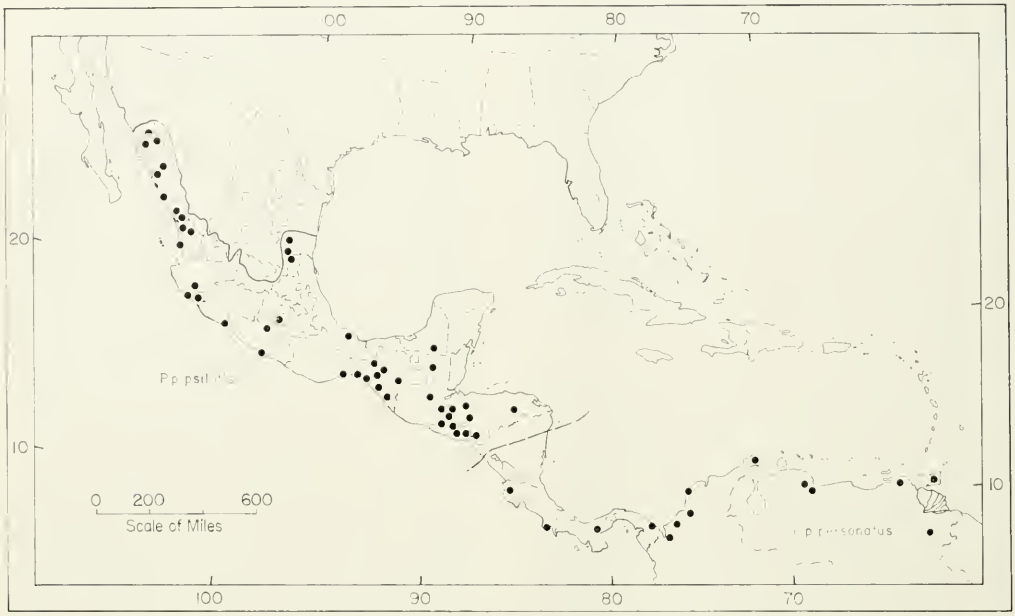


FIGURE 28. Distribution of *Pteronotus personatus*. The type locality, San Vicente, Mato Grosso, Brasil, is not shown.

formed by a thin spicule of bone (a similar condition exists in *Mormoops*; the infraorbital canal opens at the end of a short tubular canal in all other species of the genus *Pteronotus*, Fig. 18).

Relationships.—Aside from the unique characteristics described above, *personatus*, more than any other species of the genus *Pteronotus*, approximates a morphologically intermediate link between the subgenera *Phyllodia* and *Pteronotus*. Externally, *personatus* most closely resembles the Antillean species *fuliginosus* and *macleayii* that are here included with it in the subgenus *Chilonycteris*. Cranially, *personatus* resembles *P. davyi*, but differs from that species in having a narrower, less upturned rostrum; more prominent mastoid flanges; and a comparatively smaller braincase. The skull of *P. parnellii* also resembles that of *personatus*, but is more massive in structure, has a more inflated braincase, and markedly heavier dentition.

Geographic variation.—Unfortunately, most of the available material of this species is from México, thereby making difficult an accurate assessment of geographic variation within the species as a whole. Generally, as was the case in *P. parnellii*, there is a trend toward increased size, cranially as well as externally, in the southern part of the range (Table 2 and Fig. 29). The "break" between small bats in the north and larger bats of Panamá and the Caribbean coast of South America (including Trinidad) is emphasized by the paucity of specimens from certain areas in Central America. Future investigations no doubt will reveal a more extensive zone of intergradation between the two subspecies here recognized. The somewhat larger size of specimens from El Salvador (locality 10, here assigned to the subspecies *P. p. psilotis*) may result from limited gene flow along the Pacific versant of Middle America. Further comment on this point, however, must await specimens from Nicaragua and additional material from Costa Rica. Contrary to Handley (1966:759),

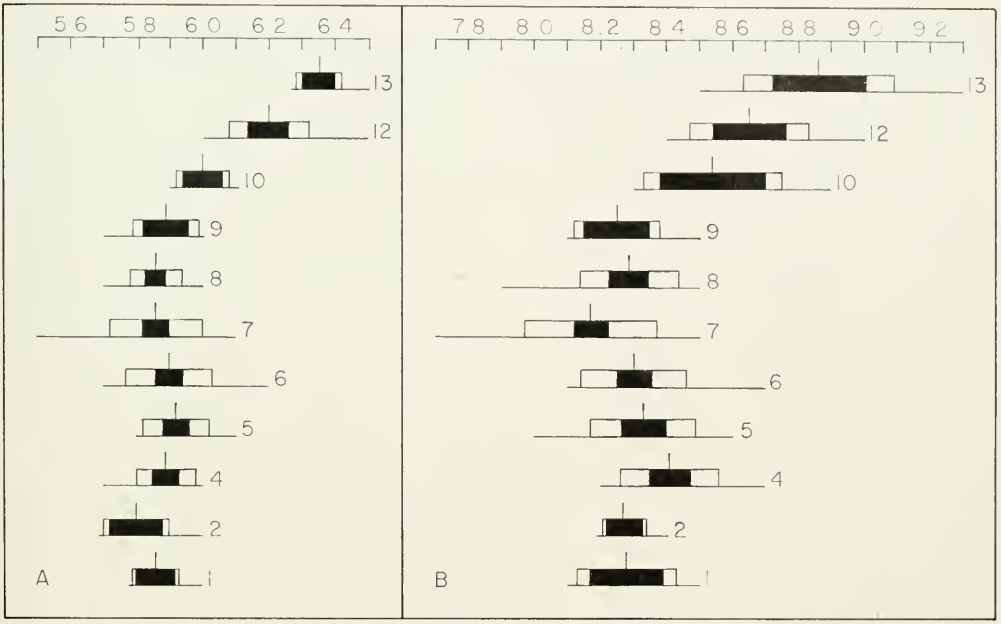


FIGURE 29. Dice-squares illustrating geographic variation in *Pteronotus personatus* from selected mainland localities. The measurements illustrated (in mm) are: A, length of maxillary toothrow; B, zygomatic breadth. See text for key to localities and figure 26 for explanation of symbols.

there seem to be sufficient differences between northern and southern populations to merit the recognition of two geographic races, as suggested by Goodwin and Greenhall (1961:323).

Key to localities used in statistical analysis of geographic variation.—1, Sinaloa; 2, Nayarit; 3, Ocampo, Tamaulipas, and vicinity of El Salto and Valle, San Luis Potosí; 4, Jalisco and Colima; 5, vicinity of Tequesquitengo, Morelos, and Teloloapan, Guerrero; 6, 3 km E San Andrés Tuxtla, Veracruz; 7, Oaxaca; 8, Lanquin Cave, Guatemala; 9, western Honduras; 10, El Salvador; 11, San José, Río Tinto, Honduras; 12, Penonomé, Panamá; 13, Cartagena, Colombia; 14, northwestern Venezuela.

Pteronotus personatus personatus (Wagner)

Chilonycteris personata Wagner, 1843, Wiegmann's Archiv für Naturgesch., 9, p. 367, 31 December, in accordance with the International Code of Zoological Nomenclature (Art. 21b, ii, p. 19).

Holotype.—Adult male, preserved in alcohol, skull not removed, Naturhistorisches Museum, Vienna, Austria (no registration number); from Mato Grosso, Brasil; obtained by Johann Natterer. Wagner (1847:185) restricted the type locality to St. Vicente, Mato Grosso, Brasil.

Distribution.—From western Costa Rica south into South America, where it occurs along the Caribbean coast, including Trinidad. Only one specimen was examined from south of the coastal region, this being from Los Patos, 28 km SE El Manteco, Bolívar, Venezuela. No other specimens, aside from the holotype, are known from the Amazon Basin (Fig. 28). Two specimens, reported as this species by Da Cunha Vieira (1942:272) from Cuiabá and Tapirapoa, Mato Grosso, Brasil, are *Pteronotus parnellii rubiginosus* (see Da Cunha Vieira, 1955:358).

Description.—Wagner (1843:367) described the holotype as follows: *"Ch. fusca, suptus dilutior, dorso piloso."* The length of forearm was given as 1.8 inches [about 46.0]. In a later paper, Wagner (1847:185-186) compared *"Ch.*

TABLE 2. Selected external and cranial measurements of several populations of *Pteronotus personatus*. Each measurement is represented by the observed range, below which is the mean, plus or minus two standard errors of the mean; superscript numbers indicate sample size if different from that given in left-hand column. See text for key to localities.

Locality	*N*	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
			Pteronotus personatus psilotis				
1	7	42.1±0.53[6]	8.3±0.11	5.8±0.10	5.9±0.06	13.7±0.06	7.4±0.08
		(41.1–42.9)	(8.1–8.5)	(5.7–6.1)	(5.8–6.0)	(13.6–13.8)	(7.2–7.5)
3	6	42.1±0.43	8.4±0.07	6.0±0.08	5.9±0.06	14.0±0.14	7.5±0.14
		(41.5–42.9)	(8.3–8.5)	(5.8–6.1)	(5.8–6.0)	(13.7–14.2)	(7.2–7.7)
5	23	42.7±0.33[24]	8.3±0.07[19]	5.9±0.04[22]	5.9±0.04[24]	13.9±0.10	7.6±0.07
		(41.1–44.4)	(8.0–8.6)	(5.7–6.0)	(5.8–6.1)	(13.4–14.4)	(7.2–7.9)
6	47	43.2±0.24	8.3±0.05	5.9±0.05	5.9±0.04	13.9±0.07	7.4±0.05
		(40.8–45.0)	(8.1–8.7)	(5.6–6.2)	(5.7–6.2)	(13.4–14.4)	(7.0–7.9)
8	29	42.7±0.35[27]	8.3±0.06	5.9±0.04[50]	5.9±0.03	13.8±0.08	7.2±0.04
		(40.8–43.9)	(7.9–8.5)	(5.7–6.1)	(5.7–6.0)	(13.2–14.1)	(7.0–7.5)
10	9	44.0±0.62	8.5±0.15[8]	6.1±0.06	6.0±0.05	14.1±0.14	7.5±0.08
		(42.6–45.2)	(8.3–8.9)	(6.0–6.2)	(5.9–6.1)	(13.8–14.5)	(7.3–7.7)
11	3	42.5±0.71	8.3±0.13	5.9±0.20	6.0±0.18	13.9±0.35	7.3±0.24
		(41.8–43.0)	(8.2–8.4)	(5.7–6.0)	(5.8–6.1)	(13.6–14.2)	(7.0–7.5)
			Pteronotus personatus personatus				
12	16	44.9±0.36[28]	8.6±0.11[10]	6.1±0.07	6.2±0.06	14.4±0.11	7.5±0.10[15]
		(43.1–46.8)	(8.4–9.0)	(6.0–6.4)	(6.0–6.5)	(14.0–14.7)	(7.1–7.8)
13	11	45.8±0.54[13]	8.9±0.14	6.3±0.08	6.4±0.04	14.6±0.15	7.6±0.10
		(44.5–47.4)	(8.5–9.3)	(6.1–6.5)	(6.3–6.5)	(14.3–15.0)	(7.3–7.9)
14	2	44.6±1.30	------	6.1±0.50	6.2±0.20	14.1±0.30	7.5±0.30
		(44.0–45.3	------	(5.9–6.4)	(6.1–6.3)	(14.0–14.3)	(7.3–7.6)

personata" to several other mormoopids and distinguished it on the basis of its small size and hair-covered back. Because Natterer's specimen had been preserved in alcohol, Wagner (1847) commented only that dorsally it was black or dark brown and ventrally it was pale brown and that the tips of the hairs of the venter were pale. Selected external measurements of the holotype, taken from Wagner (1847) unless otherwise noted are as follows (measurements originally given in inches and tenths are here converted to millimeters): length of body, 54; length of tail, 19.5; length of ear, 13; length of forearm (measured by Dilford C. Carter), 47.2; length of tibia (measured by Carter), 17.0; approximate length of skull (measured by Carter), 16.0.

Specimens herein assigned to *P. p. personatus* are large for the species, both cranially and externally. Standard external measurements of three males and one female, respectively, from Armila, San Blas, Panamá, are as follows: total length, 72, 68, 75, 73; length of tail vertebrae, 18, 18, 20, 20; length of hind foot, 11, 10, 12, 11; length of ear from notch, 17, 17, 18, 17. For additional selected external and cranial measurements, see table 2.

Dilford C. Carter (personal communication) described the color of the

holotype as "reddish brown" dorsally and paler ventrally, but also noted that it was faded. Most of the specimens of this subspecies that I have examined were in old pelage that was Ochraceous Tawny to Ochraceous Orange. Several adults from northwestern Colombia, captured in May, June, and July, were in various stages of molt. The fresh pelage is dark brown (Prout's Brown) dorsally, slightly darker (Bister) on top of the head. Ventrally, these specimens are grayish white with a buffy tinge to Cinnamon-Buff; the throat and chin are white to buffy white.

Comparisons.—From *P. p. psilotis*, the subspecies *P. p. personatus* can be distinguished on the basis of its larger cranial and external size (Table 2 and Fig. 30). Goodwin and Greenhall (1961:223) stated that their three specimens from Trinidad were smaller than Mexican specimens of this species. The two specimens from which they reported measurements are females and fall at the lower end of variation of *P. p. personatus*. However, the length of the forearm, which shows the least amount of secondary sexual variation, for these females was given as 45.7 and 44.0, which places them well within the observed variation of *P. p. personatus*. Based on the few specimens in fresh pelage, *personatus* appears to be only slightly darker than *psilotis*.

Remarks.—De la Torre (1955:697) argued that until it could be demonstrated that *psilotis* and "*personata*" were indeed conspecific, that the two taxa be maintained as full species, and this suggestion has been followed by most mammalogists. In a paper reporting on mammals from Venezuela, J. A. Allen (1911:264-265) employed the specific name "*personata*" for specimens from Aroa, Bolívar Railroad, Yaracuy, and discussed these in relation to *psilotis* Dobson, 1878, from an unknown locality (subsequently restricted to Tehuantepec, Oaxaca, México, by de la Torre, 1955:696). Allen (1911:265) quoted a portion of a letter from G. S. Miller, Jr., who had compared some of the Venezuelan material with specimens from México. In this quotation, Miller indicated that the Venezuelan material was slightly different and that he was inclined to recognize the two groups at least as subspecies. Goodwin and Greenhall (1961:223) recognized the distinctness of South American bats and applied the name *Chilonycteris personata personata* to specimens from Trinidad. They did not elucidate, however, other than to point out that "*Chilonycteris personata* Wagner, and *Chilonycteris psilotis* Dobson, have been considered as a conspecific by some authors."

Wagner (1847), in further describing Natterer's holotype of *personatus* from San Vicente, Mato Grosso, Brasil, noted its small size in comparison to "*Ch. rubiginosa*," and its apparent similarity to "*Ch. Mac-Leayii*" and "*Lobostoma quadridens*," of Gundlach (see account of *P. m. macleayii* for discussion of *quadridens*) in having four tooth-like serrations on the ears. Measurements given by Wagner (1847) for the holotype of *personatus*, some of which have been converted to millimeters and listed above, are only slightly larger than those of specimens formerly assigned to *psilotis* from northern South America, as are measurements of the holotype taken by Dilford C. Carter. There is little question in my mind that *personatus* of Wagner should be applied to specimens from northern South America, which, as noted above, are distinctly larger than bats from México and adjacent Middle America. The alternative would be to retain *personatus* as a species, known only from the holotype, and to apply the specific name *psilotis* in the manner suggested by de la Torre (1955:697), which would necessitate proposing a new subspecific name for the populations from Costa Rica, Panamá, northern South America, and Trinidad. This would lead to considerable nomenclatural confusion if I am correct

in the assumption that *personatus* and *psilotis* are conspecific.

Specimens examined (91).—COSTA RICA. *Guanacaste:* 4.4 mi S Liberia, 1 (LACM). *Puntarenas:* Rincón de Osa, Osa Productos Forestales, Camp Seattle, 35 m, 1 (LACM). PANAMA. *Coclé:* Penonomé Caves, 23 (3 MCZ, 20 USNM). *San Blas:* Armila, Quebrada Venado, 4 (USNM). COLOMBIA. *Antiogua:* Turbo, 5 (ROM). *Bolívar:* Cartagena, 28 (8 ROM, 20 USNM). *Cordoba:* Planeta Rica, S of Monteria, 4 (ROM). *Guajira:* Nazaret, 4 (ROM). *Sucre:* Tola Viejo, 5 (ROM). VENEZUELA. *Bolívar:* Los Patos, 28 km SE El Manteco, 1 (USNM). *Carabobo:* Río Yaracuy, 10 km NW Urama, 25 m, 1 (USNM). *Sucre:* La Biea, 1 (AMNH). *Yaracuy:* Minas de Aroa, Bolívar R. R., 12 (AMNH). TRINIDAD. No specific locality, 1 (USNM).

Pteronotus personatus psilotis (Dobson)

Chilonycteris psilotis Dobson, 1878, Catalogue of the Chiroptera in the . . . British Museum, London, p. 451.

Chilonycteris torrei continentis Sanborn, 1938, Occas. Papers Mus. Zool., Univ. Michigan, 373:1, 26 May. Type locality, Laguna de Zotz, Petén, Guatemala. Holotype, adult male, preserved in alcohol, skull removed, UMMZ 77085; obtained on 4 March 1935 by C. L. Hubbs and H. Van de Schalie.

Syntypes.—Adult male, preserved in alcohol, skull removed, BM 50.8.29.3, and adult female, preserved in alcohol, skull not removed, BM 50.8.29.4; from an unknown locality (restricted to Tehuantepec, Oaxaca, México, by de la Torre, 1955:696); obtained by Lt. Stricklan.

Distribution.—From southern parts of Sonora and Tamaulipas, México, southward (excluding portions of the Mexican Plateau and Yucatan Peninsula) to eastern Honduras and El Salvador (Fig. 28).

Description.—Contrary to the statement of Goodwin and Greenhall (1961: 223), this subspecies averages smaller externally and cranially than does *P. p. personatus* (Table 2 and Fig. 30). Standard external measurements (average, with extremes in parentheses) of 18 males and 12 females, respectively, from 3 km E San Andrés Tuxtla, 1000 ft, Veracruz, are as follows: total length, 66.8 (64.0-74.0), 67.1 (63.0-70.0); length of tail vertebrae, 17.0 (15.0-19.0), 17.6 (16.0-20.0); length of hind foot, 10.9 (10.0-12.0), 11.2 (10.0-12.0); length of ear from notch, 16.3 (16.0-17.0), 16.2 (16.0-17.0).

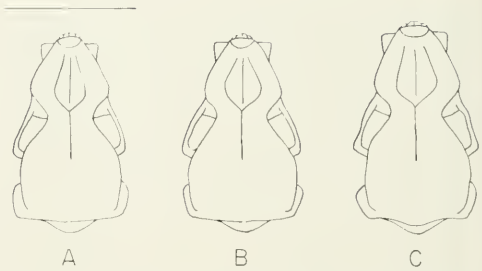


FIGURE 30. Dorsal view of skulls of *Pteronotus personatus psilotis* (A, Sinaloa; B, Guatemala) and *P. p. personatus* (C, Colombia). All specimens are adult males; horizontal line above A is 10 mm in length.

The length of forearm of the syntypes (measured by J. Knox Jones, Jr.) were approximately 41.3 for the male and approximately 43.6 for the female (measurements are approximate because forearms appeared to be partly fractured). Selected cranial measurements (taken by Jones) of the male syntype are as follows: zygomatic breadth, 8.7; breadth of braincase, 8.0; mastoid breadth, 8.9; zygorostral length, 10.0; interorbital constriction, 3.6; rostral breadth, 6.0; length of maxillary toothrow, 5.8; condylobasal length, 13.4; length of mandibular toothrow, 7.0. See table 2 for additional selected external and cranial measurements of this subspecies.

Most of the specimens of *psilotis* examined were in old pelage that ranged in color dorsally from reddish brown to Ochraceous Tawny or brilliant Ochraceous Orange. Ventrally, the pale tips of the hairs are markedly reddish and in some cases almost yellowish, evidently owing to changes with age of the pelage. In fresh pelage, these bats are gray to brownish (Snuff Brown) dorsally, with the top of the head being

somewhat darker. A pale-colored central zone is faintly discernible on the hairs of the back. Hairs of the pectoral an abdominal regions are strikingly bicolored, with brown bases (Prout's Brown to Snuff Brown) and tips that are pale grayish white or Cinnamon Buff. Two adult males from near Vaca, Sinaloa, caught in November, are dark brown dorsally and olive-brown ventrally (terminal parts of ventral hairs grayish white).

Comparisons.—For comparison with *P. p. personatus*, see preceding account.

Remarks.—The general resemblance between *P. personatus* and the Antillean *P. fuliginosus* led Sanborn (1938:1-3) to describe Guatemalan specimens as only subspecifically distinct from *Chilonycteris torrei* of Cuba (herein assigned as a subspecies of *P. fuliginosus*). He distinguished *C. t. continentis* from other mormoopids on the basis of attachment of the wing and uropatagium to the ankle and the projection of the calcar past the "free edge" of the uropatagium. The projection of the calcar in this fashion is more or less typical of the Antillean species *P. fuliginosus* and *macleayii*; it also is present, but considerably more variable, in *P. personatus*. The holotype of *continentis* and other Guatemalan specimens examined clearly are of the same subspecies as those from farther north in México.

Although there is some variation, Mexican and northern Middle American representatives of this subspecies are uniformly small in size. In southeastern Honduras and eastern El Salvador (locality 10), there is a rather marked increase in overall size possibly indicating intergradation between *psilotis* and *personatus*. Because there is a certain degree of overlap in measurements of bats from El Salvador and those from more northerly locations, I have tentatively assigned these to the subspecies *P. p. psilotis*.

Specimens examined (426).—MEXICO. *Campeche:* 65 km S, 1228 km E Escárcega, 2 (KU). *Chiapas:* 10 mi NE Mal Paso, 500 ft, 2 (TCWC); 3 mi SSE Soyoló, 3000 ft, 1 (TCWC); Santo Domingo, near Cupia, 4 km SSE Chiapa de Corzo, approx. 1300 ft, 1 (TCWC); *38 mi SSE Tuxtla Gutiérrez, 1800 ft*, 2 (TCWC); *Río Dorado, 40 mi SSE Tuxtla Gutiérrez, 1800 ft*, 2 (TCWC); 5 mi N Arriaga, 800 ft, 1 (TCWC); 10 mi S Zapaluta, 3000 ft, 2 (TCWC); 20 km SE Pijijiapan, 2 (LACM); 11 km NW Escuintla, 100 ft, 2 (LACM). *Colima:* 7 mi W, 0.5 mi S Santiago, 6 (KU); *Playa de Oro, 8 km W, 2 km S Santiago*, 16 (KU); Cueva de La Fabrica, 4 mi S Coquimatlán, 18 (LACM); Pueblo Juárez, 1 (AMNH). *Guerrero:* 12 km N Zacatula, 1 (ENCB); Río de Los Sabinos, 16 km E (by road) Teloloapan, 1040 m, 6 (IB); *10 mi E, 2 mi S Teloloapan*, 1 (KU); 2 mi NW Acapulco, 50 ft, 16 (13 KU, 3 MSU). *Jalisco:* 5 mi S Grullo, 3100 ft, 2 (KU); *Autlán, La Grana*, 12 (IB). *Morelos:* Alpuyeca, 3500 ft, 3 (TCWC); *2 km W Tequesquitengo, 1000 m*, 7 (ENCB); *Tequesquitengo*, 4 (AMNH); *3.4 km S Tequesquitengo, 840 m*, 16 (IB). *Nayarit: Huajicori, Río del Bajar*, 7 (LACM); La Cuchara, approx. 40 mi E Acaponeta, 2 (LACM); San Blas, 5 (MVZ). *Oaxaca:* San Geronimo, 1 (USNM); *6 mi NW Mixtequilla*, 3 (TCWC); Tapanatepec, 375 ft, 55 (54 AMNH, 1 KU); *10 mi S Tapanatepec*, 10 (AMNH). *San Luis Potosí:* El Salto, 1750 ft, 3 (2 AMNH, 1 KU); *1 km S El Salto*, 2 (KU); cave on Rancho Nacimiento de Río Coy, 16 mi S El Salto, 6 (4 TCWC, 2 USNM). *Sinaloa:* 0.5 mi SE Vaca, 650 ft, 2 (KU); 1 mi S, 6 mi E El Carrizo, 1 (KU); 1.5 mi N Badiraguato, 750 ft, 2 (KU); Cueva Chinacaterra, 4.5 mi S, 8 mi W Pericos, 800 ft, 3 (TCWC); La Cruz, 30 ft, 1 (KU); 1.5 mi E Concordia, 250 ft, 2 (MSU); *Chupadero, Río Pánuco, 26 mi NE Villa Unión, 800 ft*, 1 (LACM); 1 mi W Matatán, 2 (KU); 0.5 mi S Concepción, 250 ft, 4 (KU). *Tamaulipas:* 7 mi W Ocampo, 2400 ft, 1 (KU). *Veracruz:* Cueva de Laguna Encantada, 3 km ENE San Andrés Tuxtla, 1000 ft, 42 (TCWC); *3 km E San Andrés Tuxtla, 1000 ft*, 44 (KU). GUATEMALA. *Alta Verapaz:* Lanquin Cave, 1022 ft, 42 (41 KU, 1 AMNH). *Chiquimula:* Jocotán, near Chiquimula, 1350 ft, 1 (KU). *Petén:* Laguna Zotz, 1 (UMMZ). HONDURAS. *Comayagua:* 1 km W Comayagua, 580 m, 19 (TCWC). *Copán:* Ruinas de Copán, 2 (TCWC). *Ocotepeque:* 4 km N Nueva Ocotepeque, 840 m, 4 (TCWC). *Olancho:* San José Río Tinto, 340 m, 3 (TCWC). *Santa Barbara:* 5 km NE Llama, 120 m, 4 (TCWC). *Valle:* Río Laure, 10 km E San Lorenzo, 25 ft, 2 (TCWC). EL SALVADOR. *Cuscutlán:* 2 km W Suchitoto, 390 m, 2 (TCWC); San Rafael Cedros, 710 m, 2 (ROM). *Morazan:* Graveyard Mine, 1.5 mi NW Divisadero, 600 ft, 15 (MVZ). Finca El Marne, 8 km S Santa Ana, 960 m, 1 (ROM).

Additional marginal record.—*Sonora:* Río Cuchujaqui, 8 mi by road SSE Alamos, Baker and Christianson (1966:310).

Subgenus Pteronotus Gray

Type species. — *Pteronotus davyi* Gray.

Distribution.—Central Sonora and southern Tamaulipas, México, southward (excluding portions of the Mexican Plateau and Baja California) through Central America into South America, south to the Mato Grosso region of Brasil and west to the Province of Piura in northern Perú. The species *P. davyi* also occurs on Trinidad and the Lesser Antillean islands of Grenada, Dominica, Marie Galante (off Guadeloupe), and Martinique. For additional information concerning distribution, see accounts beyond and figures 33 and 35.

Description.—Size medium to large; wing membranes fused dorsally at midline, resulting in a naked-backed appearance; wing membrane and uropatagium attached to ankle by way of a long ligament (nearly half as long as tibia) that is tightly bound to tibia; labio-nasal plate moderately complex in structure, margin above each nostril ornamented by a series of irregularly shaped, wart-like tubercles, lateral spikes present on either side of nostrils (Fig. 11C); tragus moderately complex, spatulate, with prominent secondary fold and distal tip curled craniad, and with moderately long hairs ornamenting distal and cranial edges (Fig. 10, E-F); antero-medial edge of pinna smooth (lacking tooth-like serrations); ears not noticeably connected by ridge, rostral tubercle only weakly developed; pelage monocolored or only slightly bicolored dorsally (hair beneath dorsally fused wing membranes noticeably longer than that exposed in the scapular, nape, and head regions); profile of skull relatively flat, but rostrum short and noticeably upturned; forehead relatively abruptly elevated onto elongated braincase; proximal nasal root distinctly "scooped out" forming a pronounced basin; rostrum extremely broad in contrast to length as exemplified by relatively short maxillary toothrow; upper incisors reduced in size, inner pair bifurcate and with a narrow rounded heel directed toward canine, inner and outer incisors of each premaxillary compressed together, forming two groups with just the inside tips of the inner two incisors touching (this character shared with the subgenus *Chilonycteris*); diastema present between outer incisor and canine; lower incisors reduced in size and trilobed, with short rounded heel; tympanic ring large, nearly covering auditory bulla; basioccipital region between bullae, extremely broad and cup-shaped, having two shallow, oval-shaped pits into which the *M. longus capitus* inserts.

Remarks.—The fusion of the wing membranes at the dorsal midline is a peculiar feature of bats of this subgenus. Such a condition is not found in any other microchiropteran, but does exist in several megachiropterans. The functional significance of this curious feature is not known. Perhaps it is involved in the increased dissipation of heat during periods of activity. It may also function, in several ways, during flight; the most obvious of which might be to contour the posterior portion of the body or to increase the effective lifting surface. Conceivably, this arrangement also could act as a "drag chute," giving the bat a greater degree of maneuverability. These are only some possibilities and close observation of living naked-backed bats will be necessary to reveal the true functional significance of this condition.

The species of this subgenus, *P. davyi* and *suapurensis*, are morphologically similar. The primary difference between these two species is in cranial and external size, although some proportional and qualitative differences also exist (see descriptions beyond). With the exception of *P. fuliginosus* and *macleayii*, the two naked-backed species

represent the only case in the family Mormoopidae where close morphological similarity is coupled with sympatry over a broad area; *P. parnellii* and *personatus* are broadly sympatric, but, as should be apparent from the foregoing discussions, these two species are quite distinct morphologically. The pattern of intraspecific geographic variation in *davyi* and *suapurensis* suggests the possibility of character displacement: in general, *davyi* increases in overall size in progressively more southern parts of its range, whereas this trend is reversed in *suapurensis,* which increases in overall size at progressively more northerly latitudes. In every case of sympatry between these two taxa, *suapurensis* is the larger of the two. G. M. Allen (1935: 227) apparently was unaware of these trends in geographic variation and reported specimens of *suapurensis* from Penonomé, Coclé, Panamá, as *Pteronotus davyi suapurensis* because of the similarity in size between his Panamanian bats, typical *davyi* from Trinidad, and J. A. Allen's (1904) description of *suapurensis.* This is the only case known to me in which these two taxa have been considered as conspecific.

Pteronotus davyi Gray
Davy's Naked-backed Bat

(Synonymy under subspecies)

Distribution.—From central Sonora and southern Tamaulipas, México, southward (excluding portions of the Mexican Plateau and Baja California), including the Yucatan Peninsula, through Central America into South America, where its distribution is not well documented. The species occurs at least as far south as northern Perú (Piura Province) and possibly, in the Amazon Basin, to the Mato Grosso region of Brasil (see remarks below, concerning *Chilonycteris gymnonotus* Wagner, 1843). The geographic range of *P. davyi* also includes northern Venezuela, Trinidad, and Lesser Antillean islands of Grenada, Dominica, Marie Galante (off Guadeloupe), and Martinique (Fig. 33).

Description.—Size small to medium, length of forearm less than 50; wing membrane, which is fused dorsally, sparsely covered by long, irregularly-spaced hairs.

Relationships.—Pteronotus davyi is closely related to *suapurensis.* However, these two taxa are easily distinguished by cranial and external size (Tables 3 and 4 and Fig. 34). In addition, the pubescence of the dorsally fused wing membrane—shorter and denser in *suapurensis*—also separates the two. Apparently, *P. davyi* has diverged less from the main line of evolution than has *suapurensis* within the genus *Pteronotus.* As mentioned above, *davyi* somewhat resembles *P. (Chilonycteris) personatus* in size and general shape of the skull. However, other features, such as structure of the tragus and labio-nasal plate, broader and more elevated rostrum, and dorsally fused wing membranes readily distinguish the subgenus *Pteronotus* from *Chilonycteris.*

Geographic variation.—The paucity of material from Central America to the south of El Salvador and Honduras, and from South America, limits an accurate definition of geographic variation in this species. Until now, there was a sizeable gap in the known geographic range, extending from Nicaragua into South America, where the species was known only from Grenada and Dominica in the Lesser Antilles, Trinidad, and Brasil. Starrett and Casebeer (1968:7) reported material from Costa Rica and I have examined specimens from western Venezuela and Nicaragua, which suggests that the species occupies a continuous distribution from México into South America.

With the exception of the Sonoran population, *davyi* is uniformly small, both cranially and externally, throughout México. There is a gradual increase in overall size that begins in southern México (localities 9-10) and continues

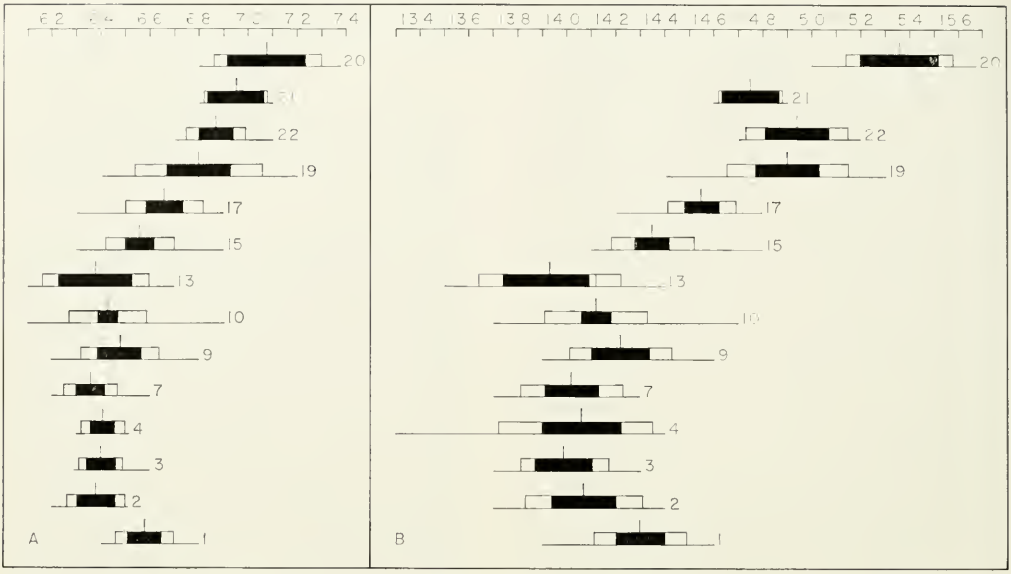


FIGURE 31. Dice-squares illustrating geographic variation of *Pteronotus davyi* from selected mainland localities (see text for key to localities). The measurements illustrated (in mm) are: A, rostral breadth; B, condylobasal length. See figure 26 for explanation of symbols.

into the adjacent region of Guatemala. In Honduras and El Salvador (localities 16-18), this increase in cranial and external proportions is considerably more pronounced than in bats to the north (Table 3 and Fig. 31). The Sonoran population (locality 1) is of interest in that these bats average comparatively larger than those from most other Mexican populations and resemble *davyi* from northern Middle America. Sinaloan bats, although generally more like typical Mexican populations, are somewhat intermediate between these and Sonoran bats.

The above features can be seen in the distance phenogram (Fig. 32) in which large-sized bats from Sonora, Morelos, and northern Middle America are grouped together in the upper couplet (localities 1, 9, and 15-18) which has a distance coefficient of 0.980. The remaining Mexican populations are grouped in the second couplet, which has a distance coefficient of 0.700. Both of these couplets are in turn lumped into a larger couplet with a coefficient of 1.330, which is widely separated (distance coefficient, 3.430) from the bottom couplet that encompasses Nicaraguan, Lesser Antillean, and South American populations (including Trinidad). In the latter couplet, *davyi* from northwestern Perú (locality 20) are segregated by a rather large distance coefficient of 1.890.

Basically, the analysis of geographic variation indicates that there are two main populations of *davyi* (contrary to the findings of Starrett and Casebeer, 1968:8), which meet along a transverse zone of intergradation that is roughly located near the northern border of Nicaragua. Judging from the material at hand, this zone appears to be extremely narrow and may represent a relatively recent zone of secondary contact between the northern and southern populations. In the northwestern extreme of the Mexican portion of the northern population, ecological as well as physiographic factors seem to have favored large size, independent of the trend toward large size observed at southern latitudes.

In the southern population, there is

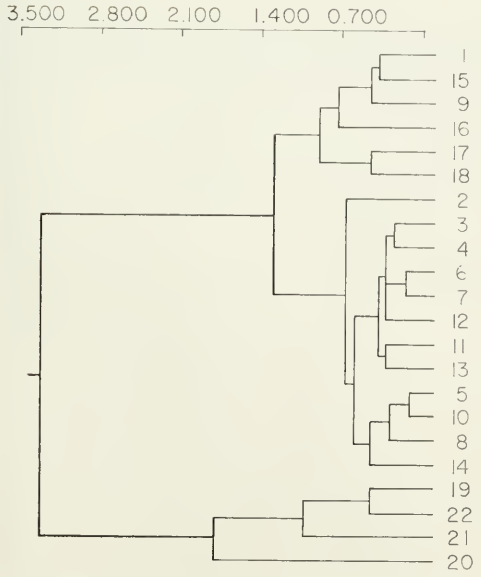


FIGURE 32. Phenogram of geographic variation of *Pteronotus davyi* computed from the distance matrix on standardized locality means and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation for this phenogram is 0.857. See text for key to localities.

a small amount of variation between bats from Dominica, Trinidad, Costa Rica, and Nicaragua. However, there is considerable difference between these bats and those from northwestern Perú. In view of the distinctness of the Peruvian bats, and the possibility that they represent an isolated population in the semiarid Pacific lowlands, west of the Andes, I have elected to recognize them as a new subspecies.

Remarks.—Wagner (1843:367) proposed the name *Chilonycteris gymnonotus* for a naked-backed bat sent to him by Johann Natterer from Cuyaba (= Cuiabá), Mato Grosso, Brasil. Later, Wagner (1847:183-185) redescribed and illustrated this species. In conjunction with the description of *Lonchorhina aurita*, Tomes (1863:83) commented that "the bottle from which this specimen [holotype of *L. aurita*] was taken contained several West Indian species, in which the *Mormops blainvillii* [probably *Mormoops megalophylla*] and the *Chilonycteris gymnonota* of Wagner were conspicuous. The latter is distinguished from other species of the genus by having the wing-membrane springing from the middle of the back, instead of the sides of the body; and there can be but little doubt that it is the *Pteronotus davyi* of Dr. Gray." This is apparently the first time *gymnonotus* was synonymized with *davyi*, an arrangement that has prevailed until now. Thomas (1892:162) restricted the type locality of *Lonchorhina aurita* Tomes, to Trinidad, which suggests that Tomes' specimens of "*C. gymnonota*" also may have come from there. At any rate, the precedent seems to have been set and *C. gymnonotus* has been consistently regarded as a synonym of *P. davyi*. J. A. Allen (1904:229) described the large naked-backed species *Pteronotus suapurensis* from Suapuré, Bolívar, Venezuela, but made no reference to *C. gymnonotus*. Examination of Wagner's (1847) comments and measurements of *gymnonotus* reveals that it is somewhat larger than typical *P. davyi*. Da Cunha Vieira (1942:268-270) reported a naked-backed bat, a female, from San Luis de Caceres, Mato Grosso, Brasil, which he assigned to *P. davyi;* length of forearm was given as 50 for this specimen. The length of forearm of the holotype of *gymnonotus* was given by Wagner (1843) as (converted) approximately 48. Dilford C. Carter (personal communication), examined the holotype of Wagner's naked-backed species and found that the forearm was approximately 51, but that both forearms were broken. The approximate length of the skull was 17.5, which is slightly larger than the holotype of *suapurensis*. The length of the maxillary toothrow of the holotype of *suapurensis* (examined by me) was 7.3, whereas Carter obtained 7.0 for the holotype of *gymnonotus*. At this point, it seems highly probable that Wagner's naked-backed bat, *P. gymnonotus*, is not a synonym of *P. davyi*, but

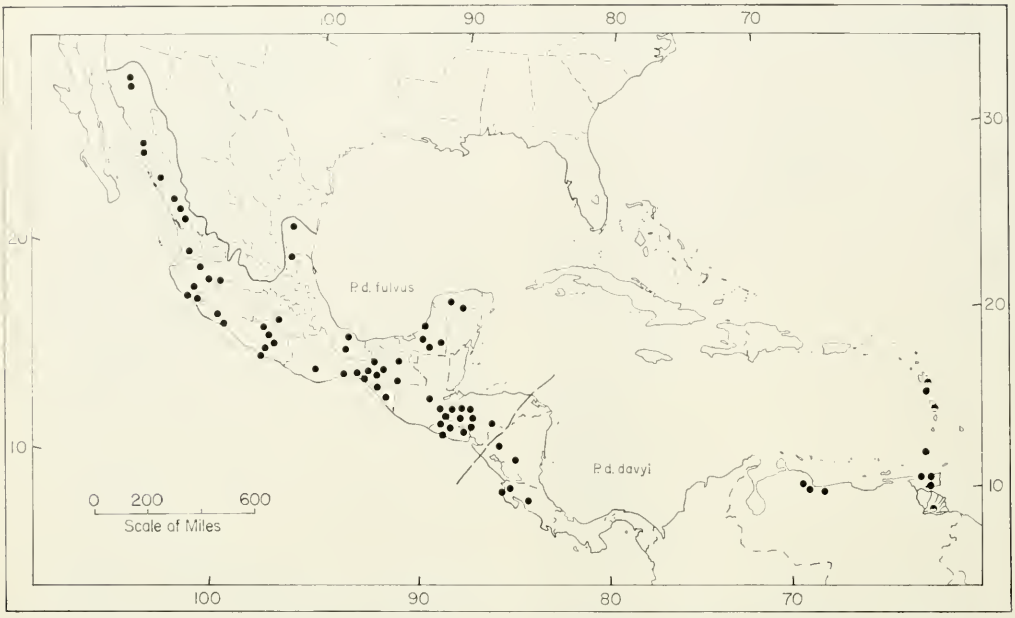


FIGURE 33. Distribution of *Pteronotus davyi*. A few localities in central South America (Brasil and Perú) are not shown, including the occurrence of the subspecies *P. d. incae*.

actually a prior description of the species known as *P. suapurensis*. However, in view of the paucity of material from the Amazon Basin, and because I have not personally examined Wagner's holotype, I tentatively retain the name *suapurensis* for the large naked-backed species and regard *gymnonotus* as a synonym of *P. d. davyi*. If the holotype of *gymnonotus* is critically compared and found to be conspecific with *suapurensis*, I would certainly advocate the recognition of *gymnonotus* as the valid name for the large naked-backed species in the interest of stability within Chiropteran nomenclature.

Key to localities used in statistical analysis of geographic variation.—1, Sonora; 2, Sinaloa; 3, Tamaulipas; 4, El Salto, San Luis Potosí; 5, Jalisco; 6, Colima; 7, vicinity of Zacatula, Acapulco, and Acahuizotla, Guerrero; 8, vicinity of Teloloapan and Colotlipa, Guerrero; 9, vicinity of Tequesquitengo, Morelos; 10, 3 km E San Andrés Tuxtla, Veracruz; 11, vicinity of Tehuantepec and Tapanatepec, Oaxaca; 12, western Chiapas; 13, central Chiapas; 14, Campeche; 15, Lanquin Cave, Guatemala; 16, eastern Honduras; 17, western Honduras; 18, El Salvador; 19, 3 mi E San Ramón, Nicaragua; 20, Piura Province, Perú; 21, Trinidad; 22, Dominica.

Pteronotus davyi davyi Gray

Pteronotus davyi Gray, 1838, Mag. Zool. Bot., 2:500, February.

Chilonycteris gymnonotus Wagner, 1843, Wiegmann's Archiv für Naturgesch., 9, p. 367, 31 December (in accordance with the International Code of Zoological Nomenclature, Art. 21b, ii, p. 19). Type locality, Cuyaba (=Cuiabá) Mato Grosso, Brasil. Holotype, adult female, preserved in alcohol, skull removed, Naturhistorisches Museum, Vienna, Austria (no registration number); obtained by Johann Natterer in February; original no. 88. See remarks in species account of *P. davyi* above.

Holotype.—Adult, sex not determined, preserved in alcohol, skull removed, BM 9.1.4.74; from Island of Trinidad; collector unknown.

Distribution.—From Nicaragua south through Central America into South America, where it is known from several localities along the Caribbean coast of Venezuela to Trinidad; also on the Lesser Antillean islands of Grenada,

TABLE 3. Selected external and cranial measurements of several populations of *Pteronotus davyi*. Each measurement is represented by the observed range, below which is the mean, plus or minus two standard errors of the mean; superscript numbers indicate sample size if different from that given in the left-hand column. See text for key to localities.

Locality	N	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
				Pteronotus davyi fulvus			
1	15	45.0±0.45[16] (43.3—46.4)	8.7±0.10 (8.3—9.0)	6.7±0.07[13] (6.5—6.9)	6.4±0.05 (6.3—6.6)	14.3±0.10[14] (13.9—14.6)	7.5±0.04 (7.4—7.6)
2	11	43.7±0.56[9] (42.3—45.2)	8.5±0.12[10] (8.3—8.8)	6.5±0.08 (6.3—6.6)	6.2±0.07 (6.0—6.4)	14.1±0.14 (13.7—14.4)	7.3±0.15[10] (7.7—7.7)
3	10	44.0±0.56 (42.5—45.2)	8.5±0.07 (8.4—8.7)	6.5±0.06[11] (6.4—6.7)	6.2±0.07 (6.0—6.4)	14.0±0.12 (13.7—14.3)	7.3±0.13 (7.0—7.6)
9	13	44.2±0.65 (42.4—46.7)	8.7±0.11 (8.3—9.0)	6.6±0.09 (6.3—6.9)	6.4±0.07 (6.2—6.6)	14.2±0.12[12] (13.9—14.6)	7.5±0.08[12] (7.3—7.8)
10	59	43.8±0.29 (40.6—46.2)	8.6±0.04[54] (8.3—9.0)	6.5±0.04 (6.2—7.0)	6.3±0.03 (6.0—6.5)	14.3±0.06[56] (13.7—14.7)	7.4±0.04[55] (7.1—7.7)
15	22	45.1±0.51[13] (43.7—46.9)	8.7±0.08 (8.4—9.1)	6.7±0.06[24] (6.4—7.0)	6.4±0.04[24] (6.2—6.7)	14.3±0.07 (14.1—14.8)	7.4±0.06 (7.2—7.6)
17	17	45.2±0.49 (43.7—47.8)	8.8±0.07 (8.5—9.0)	6.8±0.08 (6.4—7.0)	6.5±0.04 (6.4—6.6)	14.6±0.07 (14.2—14.8)	7.5±0.09 (7.1—7.8)
18	12	45.3±0.52[10] (44.3—46.7)	8.8±0.14 (8.4—9.2)	6.7±0.08 (6.5—7.0)	6.5±0.09 (6.3—6.8)	14.5±0.14 (14.2—15.1)	7.5±0.19 (6.7—8.2)
				Pteronotus davyi davyi			
19	14	46.1±0.82 (44.0—49.2)	9.0±0.13 (8.7—9.5)	6.9±0.13 (6.5—7.3)	6.7±0.07 (6.4—6.9)	14.9±0.13 (14.4—15.3)	7.7±0.15 (7.2—8.1)
21	4	47.3±2.90[3] (45.9—48.8)	9.1	7.0±0.13 (6.9—7.2)	6.8±0.10 (6.7—6.9)	14.7±0.13 (14.6—14.9)	7.8±0.24 (7.6—8.1)
22	10	46.1±0.64[5] (45.4—46.9)	9.0±0.07 (8.9—9.2)	7.0±0.07 (6.8—7.2)	6.6±0.08 (6.5—6.9)	14.9±0.13 (14.7—15.2)	7.7±0.06 (7.5—7.8)
				Pteronotus davyi incae			
20	8	49.3±0.24 (48.6—49.6)	9.3±0.08 (9.1—9.4)	7.2±0.16 (6.9—7.5)	6.9±0.08 (6.7—7.0)	15.4±0.16 (15.0—15.7)	8.1±0.11 (7.9—8.3)

Dominica, Marie Galante (off Guadeloupe), and Martinique (Fig. 33).

Description.—Size medium, both externally and cranially, for species (Table 3 and Fig. 34). Standard external measurements (average, with extremes in parentheses) of 17 males and nine females, respectively, from 8 mi E San Ramón, Matagalpa, Nicaragua, are as follows: total length, 78.3 (73.0-81.0), 79.3 (76.0-83.0); length of tail, 22.1 (18.0-24.0), 22.2 (20.0-24.0); length of hind foot, 11.2 (10.0-12.0), 11.3 (10.0-12.0); length of ear from notch, 17.3 (16.0-19.0), 17.0 (16.0-18.0). See table 3 for additional selected external and cranial measurements.

Selected cranial measurements (taken by Dilford C. Carter) of the holotype are as follows: zygomatic breadth, 9.0; breadth of braincase, 7.9; mastoid breadth, 8.7; rostral breadth, 7.2; length

of maxillary toothrow, 6.5; length of mandibular toothrow, 7.9; condylobasal length, 14.1; depth of cranium, 8.2.

Individuals taken in March from Dominica are brownish (Snuff Brown) dorsally. There is only a faint indication of color zones on the exposed hairs of the back, the basal portion being only slightly darker than the remainder of the hair. Ventrally, the pelage is markedly bicolored; the bases of the hairs are dark brown (Prout's Brown) the tips are paler, giving the venter an overall pale brown appearance. A large series collected on 9 May from near San Ramón, Nicaragua, continued individuals that were bright Ochraceous Orange in color, as were specimens of *suapurensis* captured there at the same time.

Comparisons.—See following accounts for comparisons with other subspecies.

Remarks.—The paucity of specimens of *davyi* from southern Middle America and South America unfortunately limits study of geographic variation within the species. Although, there appears to be a zone of intergradation located in northern Nicaragua and eastern Honduras and El Salvador, the Nicaraguan bats are strikingly larger in overall size than are those from more northerly populations. In Central America, these bats seem to occur mostly along the drier Pacific coast and in South America, *P. d. davyi* appears to favor the northern coastal region where conditions also tend to be somewhat arid.

This race represents the only occurrence of mormoopid bats in the Lesser Antillean islands. I suspect this invasion is relatively recent (perhaps late Pleistocene), judging from the absence of any noteworthy morphological differences between Dominican specimens and those from northeastern South America. There can be little doubt that the initial invasion of the Lesser Antilles occurred from northeastern South America or from Trinidad.

Specimens examined (171).—NICARAGUA. *Chontales:* Cuapa, 4 (KU). *Matagalpa:* 3 mi E San Ramón, 126 (KU). COSTA RICA. *Alajela:* 4.6 mi W Atenas, 1 (LACM); *road from Atenas to San Mateo,* 1 (LACM). *Guanacaste:* Playa de Coco, 1 (LACM); 5 mi N Liberia, 1 (LACM). VENEZUELA. *Carabobo:* Río Yaracuy, 10 km NW Urama, 25 m, 1 (USNM). *Distrito Federal:* El Limón, 3 km S, 46 km W Caracas, 380 m, 1 (USNM). *Sucre:* Ensenada Cauranta, 7 km N, 5 km E Guiria, 1 m, 1 (USNM). *Yaracuy:* Minas de Aroa, Bolívar R. R., 1 (AMNH). TRINIDAD. Port of Spain, 9 (1 AMNH, 7 FMNH, 1 MCZ); *Carenage,* 2 (AMNH); *Nariva,* 1 (AMNH); *Aripo,* 1 (AMNH); Siparia, 1 (AMNH). DOMINICA. *St. George:* Roseau, *ca.* 50 ft, 2 (USNM). *St. Luke: South Chiltern Estate, ca. 1300 ft,* 2 (USNM). *St. Patrick: Grand Bay, sea level,* 7 (USNM). No specific locality, 8 (5 FMNH, 3 USNM). GRENADA. No specific locality, 1 (BM).

Additional marginal records.—LESSER ANTILLES (Jones and Phillips, 1969). Marie Galante (off Guadeloupe); Martinique. VENEZUELA. Araguaimujo, Territorio Delta Amacuro, Pirlot (1965:379).

Pteronotus davyi fulvus (Thomas)

Ch[ilonycteris]. Davyi fulvus Thomas, 1892, Ann. Mag. Nat. Hist., ser. 6, 10:410, November.

Pteronotus davyi fulvus Miller, 1912, Bull. U. S. Nat. Mus., 79:33, 31 December.

Pteronotus suapurensis calvus Goodwin, 1958, Amer. Mus. Novit., 1871:1, 26 February. Type locality, Tehuantepec, Oaxaca, México. Holotype, adult male, skin and skull, AMNH 175100; obtained by Thomas MacDougall on 15 August 1956; original no. 1729.

Holotype.—Adult male, skin and uncleaned skull, BM 93.2.5.24; from Las Peñas, Jalisco, México; obtained by A. C. Buller on 20 November 1891.

Distribution.—From southern parts of Sonora and Tamaulipas México, southward (excluding portions of Mexican Plateau and Baja California), including the Yucatan Peninsula, to eastern Honduras and El Salvador (Fig. 33).

Description.—Size, small for the species (Table 3 and Fig. 34). Standard external measurements (average, with extremes in parentheses) of 13 males and 11 females, respectively, from 3 mi

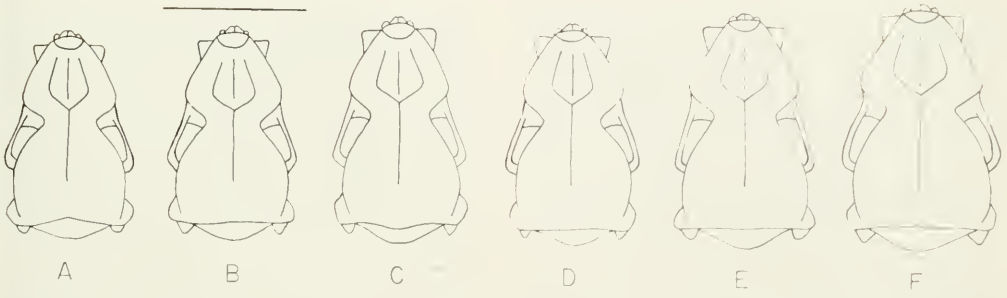


FIGURE 34. Dorsal view of skulls of *Pteronotus davyi fulvus* (A, Sinaloa; B, Guatemala), *P. d. davyi* (C, Nicaragua; D, Dominica Island), *P. d. incae* (E, Suyo, Perú), and *Pteronotus suapurensis* (F, Nicaragua). All specimens are adult males; horizontal line above B is 10 mm in length.

N El Jícaro, Juchitán, Oaxaca, are as follows: total length, 73.1 (71.0-75.0), 72.7 (71.0-75.0); length of tail, 21.5 (20.0-23.0), 21.7 (20.0-23.0); length of hind foot, 11.0 (all individuals); length of ear from notch, 17.9 (17.0-18.0), 17.7 (17.0-18.0). Additional selected external and cranial measurements are given in table 8. Length of forearm of the holotype is 43.5, and selected cranial measurements (taken by J. Knox Jones, Jr.) are as follows: zygomatic breadth, 8.2; mastoid breadth, 8.4; rostral breadth, 6.5; length of maxillary toothrow, 6.3.

Dorsally the color of this subspecies ranges from bright Ochraceous Orange to dark brown. October-taken individuals from 15 km W Ameca, Jalisco, are in fresh pelage and the exposed pelage on the back is dark brown (Bister to Prout's Brown); color zones on the hairs are not readily apparent. Pelage of the pectoral and abdominal regions is grayish white. The basal half of these hairs is dark brown and the tips are grayish white or buffy white.

Comparisons.—From *P. d. davyi,* the subspecies *P. d. fulvus* may be recognized easily on the basis of smaller size even though *fulvus* becomes somewhat larger in the southern part of its range (Honduras and El Salvador). Skulls of *P. d. davyi* are longer and broader than those of *P. d. fulvus* and, in direct comparison, appear to be more robust (Fig. 34).

Remarks.—After examining the holotype of *Pteronotus suapurensis calvus* Goodwin, 1958, I concluded that it is a large individual of *P. d. fulvus.* Goodwin evidently now shares this view, because he (1969:55) placed *P. s. calvus* in the synonymy of *P. d. fulvus.*

Mexican populations (excluding Sonoran bats) show a relatively small amount of geographic variation (Fig. 31, localities 2-13). This same situation also seems to apply to populations from the northern part of the Yucatan Peninsula, although only a few individuals were available for study from that region. In northern Middle America, bats of this subspecies gradually increase in size as they approach a narrow zone of intergradation with *P. d. davyi* in northern Nicaragua and eastern Honduras and El Salvador. The exact nature of gene flow between these two races in this region is not clear.

One of the most curious features of the geographic variation within this subspecies is the marked increase in overall size of the bats from Sonora (locality 1 in table 3 and figure 31), where males and females also exhibit the greatest amount of secondary sexual variation (Table 1). As discussed in the account of *Pteronotus parnellii mexicanus,* this part of the geographic range of the genus *Pteronotus* is at the northern and arid extreme of the Neotropical environment. In this region, factors such as suboptimal habitat and possibly

the presence (or the absence) of other insectivorous competitors may in some way influence the size of mormoopids. In *parnellii* the trend was toward smaller size, whereas with *davyi* the trend has favored large size with a greater degree of sexual dimorphism. The break between Sonoran and Sinaloan populations may be somewhat exaggerated owing to the way in which Sinaloan samples were grouped but, in any event, the trend in the geographic variation appears to be real and certainly warrants further investigation.

Specimens examined (597).—MEXICO. *Campeche:* 5 km S Champotón, 10 mi, 2 (KU); Apozote, 1 (USNM); *1 km N, 13 km W Escárcega, 65 m,* 2 (KU); *12 km W Escárcega,* 2 (KU); 105 km E Escárcega, 1 (KU); La Tuxpeña, 2 (USNM). *Chiapas:* Palenque, 1 (FMNH); 6 km NE Mal Paso, 400 ft, 1 (TCWC); Santo Domingo, near Cupia, 4 km SSE Chiapa de Corzo, 1300 ft, 7 (TCWC); Tuxtla Gutiérrez, 1 (USNM); *3 mi SE Tuxtla Gutiérrez,* 1 (AMNH); *35 mi SSE Tuxtla Gutiérrez, 2200 ft,* 1 (TCWC); *Río Dorado, 40 mi SSE Tuxtla Gutiérrez, 1800 ft,* 1 (TCWC); 13 mi SW Las Cruces, 7 (KU); *15 mi SW Las Cruces,* 1 (KU); 10 mi S Zapaluta, 3000 ft, 1 (TCWC); 8 mi N Arriaga, 2500 ft, 1 (TCWC); *6 mi N Arriaga, 600 ft,* 4 (TCWC); *5 mi N Arriaga, 800 ft,* 3 (TCWC); 5 km SE Pijijiapan, 100 ft, 4 (TCWC); 11 km NW Escuintla, 100 ft, 1 (LACM); *1.8 mi W Ixhuatán,* 1 (AMNH). *Colima:* 7 mi W, 0.5 mi S Santiago, 15 (KU); *Playa de Oro, 8 km W, 2 km S Santiago,* 2 (KU); *Punta Peña Blanca,* 3 (MSU); 4 km S Coquimatlá, 10 (LACM); *El Mixcoate, 9 km W Pueblo Juárez, 1347 m,* 11 (IB). *Guerrero:* 2 mi S, 10 mi E Teloloapan, 20 (10 IB, 10 KU); 12 km N Zacatula, 21 (ENCB); Mexcala, 2 (TCWC); Grutas de Juxlahuaca, 4 mi N Colotlipa, 3 (1 KU, 2 TCWC); *4 km NE Colotlipa, 1100 m,* 7 (ENCB); Acahuizotla, 2800 ft, 7 (TCWC); 2 mi NW Acapulco, 50 ft, 12 (11 KU, 1 MSU). *Jalisco:* 15 km W Ameca, 4200 ft, 1 (KU); El Zapote, 3 (IB); 0.5 km N, 3 km W Jamay, 1650 m, 22 (18 ENCB, 4 IB); 5 mi S Grullo, 3100 ft, 1 (KU). *Michoacán:* 7 mi S Tumbiscatio, 2700 ft, 1 (KU); Lake Chapala, 6 (AMNH). *Morelos:* 2 km W Tequesquitengo, 1000 m, 10 (ENCB); *3.4 km S Tequesquitengo, 840 m,* 6 (IB). *Nayarit:* 2 mi S Compostela, 2900 ft, 1 (KU). *Oaxaca:* 18 mi NW Sola de Vega, 1 (AMNH); *5 mi N Juchatengo,* 2 (CAS); 3 mi NE Jícaro, Juchitán, 24 (AMNH); *Tehuantepec,* 19 (AMNH); *6 mi NW Mixtequilla,* 3 (TCWC); 4 mi E Tapanatepec, 800 ft, 2 (TCWC); *10 mi S Tapanatepec,* 3 (AMNH). *San Luis Potosí:* El Salto, 7 mi N Naranjo, 26 (AMNH). *Sinaloa:* 1 mi S, 6 mi E El Carrizo, 2 (KU); 1 mi E Sinaloa, 180 ft, 1 (KU); La Chinacatera, Monte Largo, 23 km W Pericos, 11 (IB); San Juan, 8 mi S San Ignacio, 1 (KU); Pánuco, 2050 ft, 9 (KU); 3 mi SE Plomosas, 4000 ft, 1 (KU). *Sonora:* 13 mi S Carbó, 1200 ft, 7 (TCWC); *14 mi SE Carbó, 1500 ft,* 4 (USNM); *Cueva del Tigre, 14.9 mi SE Carbó,* 14 (8 LACM, 6 USNM); *20 mi SE Carbó, 2700 ft,* 2 (LACM); Rancho Banachari, 10 mi N Matape, 2700 ft, 1 (MVZ). *Tamaulipas:* Rancho Santa Rosa, 25 km N, 13 km W Ciudad Victoria, 260 m, 10 (KU); *Cueva de Los Trocones, 7.5 km W Ciudad Victoria,* 6 (IB). *Veracruz:* Cueva de Laguna Encantada, 3 km ENE San Andrés Tuxtla, 1000 ft, 46 (TCWC); *3 km E San Andrés Tuxtla, 1000 ft,* 45 (KU); Achotal, 1 (FMNH). *Yucatán:* Hoctun Cave, 14 (MVZ); Chichén Itzá, 1 (FMNH). GUATEMALA. *Alta Verapaz:* Lanquin Cave, 1022 ft, 50 (KU); *1 mi W Lanquin, 2000 ft,* 5 (TCWC). *Chiquimula:* Jocotán, near Chiquimula, 2 (KU). HONDURAS. *Comayagua:* Comayagua, 580 m, 10 (TCWC). *Copán:* Ruinas de Copán, 3 (TCWC). *El Paraiso:* 1 km SE Danli, 780 m, 1 (TCWC); *Chichicaste, 480 m,* 1 (TCWC). *Intibucá:* La Esperanza, 1660 m, 1 (TCWC). *La paz:* Cueva del Viejo, 2 mi W La Paz, 1800 ft, 13 (TCWC). *Ocotepeque:* Ocotepeque, 840 m, 1 (TCWC). *Santa Barbara:* 2 km S San Nicolas, 660 m, 12 (TCWC); *7 km N Santa Barbara, 120 m,* 1 (TCWC). *Yoro:* Subirana, 2800 ft, 7 (MCZ). El SALVADOR. *Cuscatlán:* 2 km W Suchitoto, 390 m, 3 (TCWC); San Rafael Cedros, 710 m, 2 (ROM). *La Libertad:* 5.1 km E La Libertad, 15 m, 1 (TCWC). *La Unión:* Tabanco, 650 ft, 14 (MVZ). *Morazán:* Encuentros Mine, 3 mi W Divisadero, 700 ft, 1 (MVZ). *Santa Ana:* Finca El Marne, 8 km SW Santa Ana, 960 m, 3 (ROM).

Pteronotus davyi incae new subspecies

Holotype.—Adult male, skin and skull, TCWC 11638; from 4 mi W Suyo, 1000 ft, Piura Province, Perú; obtained by Dilford C. Carter on 28 July 1964, original no. 5313.

Distribution.—Known only from northwestern Perú [not mapped].

Description.—Size, externally and cranially large for the species (Table 3 and Fig. 34). Standard external measurements of the holotype followed by those of two other adult males from the type

locality are as follows: total length, 84, 76, 82; length of tail, 25, 21, 25; length of hind foot, 9, 9, 9; length of ear from notch, 18, 17, 17. Selected external and cranial measurements of the holotype are as follows: length of forearm, 49.3; zygomatic breadth, 9.4; breadth of braincase, 8.4; mastoid breadth, 9.7; zygorostral length, 11.8; interorbital breadth, 4.0; rostral breadth, 7.5; length of maxillary toothrow, 7.0; length of mandibular toothrow, 8.1; condylobasal length, 15.7; depth of cranium, 8.0.

The holotype and type series, captured on 28 July, appear to be in fresh pelage, which is pale grayish brown (Dusky Drab) dorsally; color zones are not apparent on the exposed hairs of the back. The pectoral and abdominal regions are grayish white (Mouse Gray), whereas the throat and chin are somewhat paler. A December-taken male and a January-taken female from northwestern Perú, are Ochraceous Orange in color.

Comparisons.—From *P. d. davyi* and *P. d. fulvus*, the new subspecies is easily discernible on the basis of larger cranial and external size (Table 3 and Fig. 31). In addition to being longer, the skull of *incae* is decidedly broader (especially the rostral portion) than either that of *davyi* or *fulvus*. Although, it is difficult at this time to evaluate color accurately in these bats, *incae* appears to be somewhat paler than either of the other two races.

From *P. suapurensis*, specimens of *P. d. incae* can be easily distinguished by smaller cranial and external size and the long and scattered hairs on the dorsally fused wing membrane, in comparison to the short, densely spaced hairs of *suapurensis*.

Remarks.—Bats of this subspecies appear to be isolated on the western side of the Andes in northwestern Perú and there seem to be several possible routes by which they could have arrived in this region. One of these may have been through migration along the narrow corridor formed by the Pacific versant of the Andes in Colombia and Ecuador. Haffer (1967a:327) and Chapman (1926) suggested that part of the bird fauna of the arid Pacific coast of Colombia and Ecuador may have used this route before tropical forest developed at the beginning of the Pleistocene. The development of such a forest probably blocked subsequent dispersal of non-forest species along this route. Other alternatives involve trans-Andean crossings along several arid intermontane valleys in Ecuador and northern Perú. Of these, there seem to be only two valleys through which these bats could have passed in order to gain access to low passes over which such a crossing could have occurred. One of these passes is located between the upper Patía and Cauca valleys in southern Colombia and northern Ecuador. This route may have been used by *Mormoops megalophylla*, but as yet *P. davyi* is not known from this region. The other and perhaps more feasible route in the case of *davyi* may have been through the valley of the Río Marañón from the Amazon lowlands during an arid epoch, thence up the connecting valley of the Río Huancabamba to the low pass at its headwaters. The passes in both of these regions are relatively low and the landmass over which a migrant would have passed is rather narrow (Tuttle 1970:54). In addition, both regions are low enough to have been equitable during drier periods of the Pleistocene. Considerably more needs to be known about the Chiropteran fauna of Colombia and Ecuador, particularly in these intermontane valleys, along the eastern slopes of the Andes and the adjacent Amazonian lowlands.

The subspecies name *incae* is proposed to commemorate the civilization of the Inca that was once centered in the region of northwestern Perú.

Specimens examined (15).—PERU [localities not mapped]. *Cajamarca:* Jaen, 1 (AMNH). *Piura:* 4 mi W Suyo, 1000 ft, 3

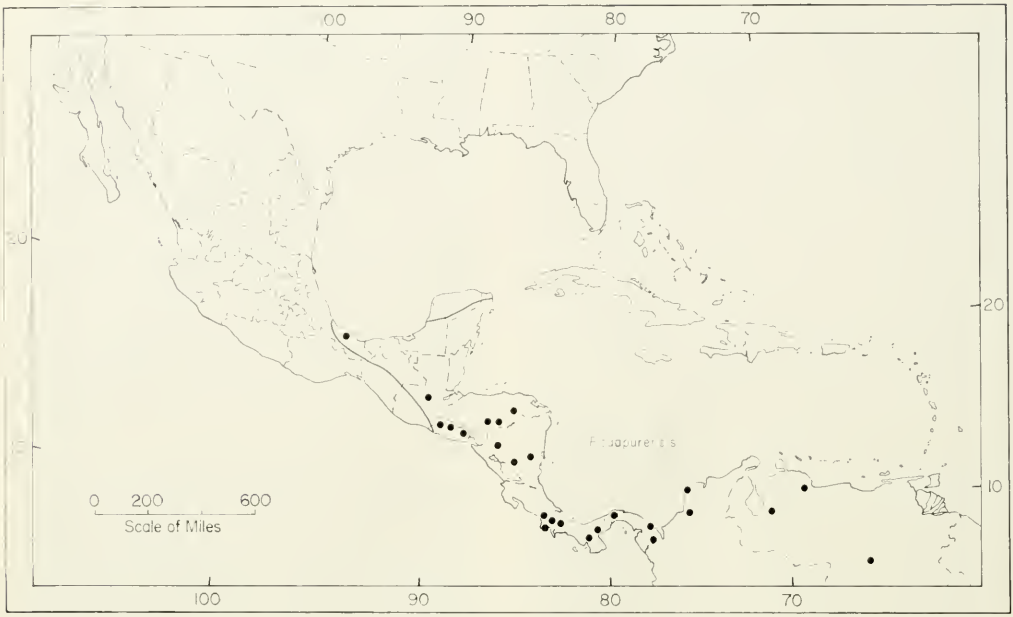


FIGURE 35. Distribution of *Pteronotus suapurensis*. A few locations in South America (Perú) are not shown.

(TCWC); Hacienda Bigotes, Salitral, 7 (FMNH); Huancabamba, 2 (AMNH); Canchaque, 2 (FMNH).

Pteronotus suapurensis (J. A. Allen)
BIG NAKED-BACKED BAT

Dermonotus suapurensis J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., 20:229, 20 June.

Pteronotus suapurensis J. A. Allen, 1911, Bull. Amer. Mus. Nat. Hist., 30:265, 2 December.

Pteronotus suapurensis centralis Goodwin, 1942, Jour. Mamm., 28:88, 16 February. Type locality Matagalpa, 3000 ft, Matagalpa, Nicaragua. Holotype, adult, sex unknown, skin and skull, AMNH 33193; obtained by W. B. Richardson on 10 November 1911.

Holotype.—Adult female, skin and skull, AMNH 17573; from Suapuré, Bolívar, Venezuela; obtained by S. M. Klages on 26 October 1901.

Distribution.—From near San Andrés Tuxtla, Veracruz, México, southward through northern Guatemala into Central America and South America, where it occurs, at least as far south as Tingo María, Perú; possibly to the Mato Grosso region of Brasil (see remarks under *Pteronotus davyi* concerning *Chilonycteris gymnonotus* Wagner, 1843); and west of the Andes in Piura Province, Perú (Fig. 35).

Description.—Size medium to large, both externally and cranially. Standard external measurements (average, with extremes in parentheses), for 10 males and three females, respectively, from 3 mi E San Ramón, Matagalpa, Nicaragua, are as follows: total length, 89.7 (86.0-93.0), 90.7 (89.0-92.0); length of tail vertebrae, 24.8 (21.0-27.0), 24.7 (24.0-26.0); length of hind foot, 12.1 (11.0-13.0), 12.7 (12.0-13.0); length of ear from notch, 18.6 (18.0-20.0), 18.3 (17.0-19.0). Additional selected external and cranial measurements are given in table 4. The wing membranes are fused on the dorsal midline and are covered with many short hairs giving the back a "velvety" appearance.

Specimens collected on 9 May near San Ramón, Nicaragua, were in bright Ochraceous Orange pelage as were individuals of *P. davyi* captured at the same time. Two females taken in Janu-

TABLE 4. Selected external and cranial measurements of several populations of *Pteronotus suapurensis*. Each measurement is represented by the observed range, below which is the mean, plus or minus two standard errors of the mean; superscript numbers indicate sample size if different from that given in left-hand column. See text for key to localities.

Locality	*N* and Sex	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
				Pteronotus suapurensis			
1	1 ♂	53.7	10.5	8.0	7.5	16.4	8.8
2	2 ♀	54.1, 53.5	10.4, 10.1	8.2, 7.6	7.3, 7.5	16.2, 16.2	8.6, 8.5
3	5 ♀	54.0±0.50 (53.1—54.5)	10.3±0.10 (10.1—10.4)	7.9±0.19 (7.7—8.2)	7.5±0.14 (7.4—7.7)	16.4±0.29 (16.1—16.8)	8.6±0.16 (8.4—8.8)
4	28 ♂	52.6±0.31[26] (51.1—54.2)	10.4±0.06 (10.2—10.8)	7.9±0.06 (7.7—8.2)	7.5±0.05 (7.3—7.7)	16.4±0.06 (16.1—16.7)	8.8±0.06 (8.5—9.2)
	37 ♀	53.6±0.39 (50.8—56.0)	10.4±0.06 (10.0—10.6)	7.9±0.06 (7.6—8.2)	7.5±0.04 (7.2—7.8)	16.4±0.06 (15.7—16.9)	8.8±0.06 (8.3—9.0)
5	10 ♂	53.1±0.57 (52.1—55.0)	10.5±0.04 (10.4—10.6)	8.0±0.05 (7.9—8.2)	7.6±0.06 (7.5—7.8)	16.5±0.11 (16.3—16.8)	8.9±0.19[8] (8.7—9.5)
	4 ♀	53.2±1.36 (51.4—54.7)	10.4±0.31[3] (10.1—10.6)	7.9±0.16 (7.7—8.1)	7.5±0.06 (7.5—7.6)	16.4±0.14 (16.2—16.5)	8.8±0.20[3] (8.6—8.9)
6	1 ♂	52.7,52.0,54.3[3]	10.1	7.7	7.4	16.4	8.6
	7 ♀	52.6±0.01[5] (50.9—53.6)	10.3±0.13[5] (10.1—10.5)	7.7±0.20[6] (7.5—8.2)	7.5±0.13 (7.2—7.7)	16.3±0.14 (16.0—16.5)	8.6±0.12 (8.4—8.9)
7	33 ♂	51.2±0.45[34] (49.0—54.0)	10.2±0.06 (9.9—10.5)	7.8±0.06 (7.4—8.1)	7.4±0.04 (7.1—7.7)	16.2±0.09[30] (15.6—16.7)	8.6±0.06 (8.3—9.1)
	19 ♀	53.3±0.48[18] (51.2—54.7)	10.2±0.07 (9.9—10.6)	7.8±0.07 (7.6—8.0)	7.5±0.06 (7.3—7.8)	16.2±0.11 (15.8—16.6)	8.5±0.08 (8.1—8.8)
8	15 ♂	51.2±0.49[15] (50.2—53.5)	10.2±0.09 (9.9—10.5)	7.7±0.08[17] (7.5—8.0)	7.4±0.03[19] (7.3—7.5)	16.2±0.11[16] (15.7—16.6)	8.6±0.12 (8.2—9.0)
	10 ♀	52.9±0.77[8] (51.1—54.3)	10.1±0.10 (9.9—10.4)	7.7±0.10[11] (7.5—8.0)	7.4±0.09[11] (7.2—7.6)	16.1±0.14 (15.7—16.4)	8.3±0.13 (8.0—8.6)
9	7 ♂	53.0±0.87 (51.5—54.8)	10.4±0.14 (10.2—10.6)	7.9±0.13 (7.6—8.1)	7.6±0.11 (7.3—7.7)	16.5±0.11 (16.3—16.7)	8.7±0.13 (8.5—9.0)
	5 ♀	53.8±0.93 (52.7—55.4)	10.3±0.17 (10.0—10.5)	8.0±0.17 (7.8—8.3)	7.6±0.04 (7.5—7.6)	16.4±0.05 (16.3—16.4)	8.6±0.10 (8.5—8.8)
10	4 ♂	51.2±1.59 (49.8—52.7)	10.1±0.07[3] (10.1—10.2)	7.7±0.14 (7.5—7.8)	7.2±0.13 (7.1—7.4)	15.7±0.45 (15.2—16.1)	8.6±0.16 (8.4—8.8)
	8 ♀	52.1±0.61 (50.9—53.2)	10.0±0.13 (9.6—10.2)	7.5±0.15 (7.2—7.8)	7.3±0.09 (7.1—7.5)	15.7±0.17[7] (15.5—16.1)	8.4±0.17[7] (8.0—8.5)
11	1 ♀	51.6	10.1	7.7	7.3	15.6	8.5
12	6 ♂	52.1±1.77 (50.8—53.3)	10.2±0.13 (10.1—10.5)	7.8±0.09[7] (7.6—7.9)	7.4±0.08[7] (7.3—7.6)	16.3±0.12 (16.1—16.5)	8.8±0.12 (8.6—9.0)
13	2 ♀	51.0, 50.5	9.5, 9.7	7.2, 7.2	6.8, 6.9	15.3, 15.5	8.3, 8.4

ary from Lanquin Cave, Alta Verapaz, Guatemala, are dark brown dorsally and ventrally. On the venter, there is a pale buffy-white wash, the chin and throat being somewhat darker.

Relationships.—Pteronotus suapurensis can be distinguished from *P. davyi*, the only other species of the subgenus, on the basis of larger cranial and external size as well as noticeably greater pubescence on the dorsally fused wing membrane.

Geographic variation.—There are so few specimens of this species presently available in collections that an accurate and meaningful analysis of geographic variation is not yet possible. Several sizable samples were examined from Central America, but only a few individuals are known from South America.

Whether or not the holotype of *P. suapurensis* (a rather small adult female) is truly representative of the populations of the Amazon Basin cannot be assessed in the absence of other comparative specimens from this critical region. It appears that there is a general geographic trend in the species toward larger overall size at progressively more northerly localities, the largest individuals occurring in Nicaragua, El Salvador, Honduras, and Guatemala. Bats of this species from Costa Rica and Panamá are only slightly smaller than those to the north, and slightly larger than individuals in a small sample from Minas de Aroa, Bolívar R. R., Yaracuy, Venezuela. The Venezuelan bats, however, frequently fall into non-significant subsets of means with both Nicaraguan and Panamanian samples; in most instances Panamanian specimens are intermediate in size between those from Venezuela and Nicaragua. The few specimens examined from Tingo María and Loreto, Perú, closely resembled Panamanian specimens although averaging somewhat smaller in cranial and external size.

Two females from Huancabamba, Piura, Perú, are slightly smaller than bats from Tingo María and Loreto and may represent an isolated population. However, because the geographic variation is slight between the few sizable samples of the species currently available, it seems best to treat the species as monotypic, a course followed by Felten (1956:77-78), Davis and Carter (1964: 377), Jones (1966:449), and Starrett and Casebeer (1968:9). Additional material from South America, may indicate that two or more geographic races warrant recognition.

Key to localities used in statistical analysis of geographic variation.—1, Cueva Laguna Encantada, 3 km ENE San Andrés Tuxtla, Veracruz; 2, Lanquin Cave, Guatemala; 3, Honduras; 4, vicinity of Divisadero, El Salvador; 5, 3 mi E San Ramón, Nicaragua; 6, southern Costa Rica; 7, Penonomé, Panamá; 8, Chilibrillo, Panamá; 9, Armila, Panamá; 10, Minas de Aroa, Venezuela; 11, Suapurá, Venezuela; 12, Tingo María, Perú; 13, Piura Province, Perú.

Specimens examined (344).—MEXICO. *Veracruz:* Cueva Laguna Encantada, 3 km ENE San Andrés Tuxtla, 1000 ft, 1 (TCWC). GUATEMALA. *Alta Verapaz:* Lanquin Cave, 1022 ft, 2 (KU). HONDURAS. *El Paraiso:* Chichicaste, 480 m, 2 (TCWC). *Francisco Morazán:* 2 mi S Zamorano, 1 (TCWC). *Olancho:* San José, Río Tinto, 340 m, 5 (TCWC). EL SALVADOR. *Cuscatlán:* 2 km W Suchitoto, 390 m, 45 (TCWC); *Suchitoto, 400 m*, 2 (ROM); *San Rafael Cedros, 710 m*, 1 (ROM). *La Unión:* Tabanco, 650 ft, 3 (MVZ). *Morazán:* Graveyard Mine, 1.5 mi NW Divisadero, 600 ft, 17 (MVZ). *Santa Ana:* Finca El Marne, 8 km S Santa Ana, 960 m, 1 (ROM). NICARAGUA. *Chontales:* Cuapa, 1 (KU). *Matagalpa:* Matagalpa, 1 (AMNH); *3 mi E San Ramón*, 13 (KU). *Zelaya:* Cara de Mono, 50 m, 4 (KU); 10 km W Rama, 40 m, 1 (TCWC). COSTA RICA. *Puntarenas:* 35 mi S San Isidro, Río Ceiba, 1 (LACM); Rincón de Osa, Oso Productos Forestales airstrip, 35 m, 2 (UMMZ); 2.7 mi N Villa Neilly, 6 (LACM); *Villa Neilly*, 2 (LACM). PANAMA. *Canal Zone: Madden Dam*, 1 (USNM). *Chiriquí:* Cerro Punta, Casa Tilley, 1 (USNM); *Bambito, 35 km N Concepción, 6200 ft*, 2 (TCWC); *4 mi from El Volcán*, 1 (ANSP); *San Vicente*, 1 (USNM). *Coclé:* Penonomé, 118 (58 FMNH, 1 LACM, 11 MCZ, 23 UMMZ, 25 USNM). *Darién:* Tacarcuna Camp, 3200 ft, 2 (USNM). *Panamá:* Chilibrillo Caves, 26 (USNM); *Chilibre*, 8 (USNM). *San Blas:* Armila, Quebrada Venado, 10 (USNM). *Veraguas:* 3 mi E Soná, 100 ft, 1 (USNM). COLOMBIA.

Bolívar: Cartagena, 36 (1 ROM, 35 USNM). *Sucré:* Tolu Viejo, 3 (USNM). VENEZUELA. *Bolívar:* Suapuré, 1 (AMNH). *Trujillo:* Agua Viva, 18 km N Valera, 164 m, 2 (USNM). *Yaracuy:* Minas de Aroa, Bolívar R. R., 11 (AMNH). PERU [localities not mapped]. *Huánuco:* 2 mi N Tingo María, 2000 ft, 6 (TCWC). *Loreto:* Yarinacocha, Río Ucayalí, 1 (FMNH). *Piura:* Huancabamba, 2 (FMNH).

Genus Mormoops Leach
Ghost-faced Bats

Mormoops Leach, 1821, Trans. Linn. Soc., 13, p. 76. See remarks below concerning the use of the generic name *Mormoops.*

Aëllo Leach, 1821, Trans. Linn. Soc., 13, p. 70 (type *Aëllo cuvieri* Leach).

Type species.—*Mormoops blainvillii* Leach, 1821.

Distribution.—Humid to arid and semi-arid regions, usually below 3000 meters, from southwestern Texas and southern Arizona, through México (including Baja California, Mexican Plateau, and Yucatan Peninsula) into Central America as far as eastern Honduras and El Salvador. Members of this genus have not yet been reported from Nicaragua, Costa Rica, or Panamá. In South America, *Mormoops* is known from the Caribbean coast of Colombia and Venezuela, Trinidad, the Dutch West Indies, and as far south as La Paz, Carchí Province, Ecuador. The genus is represented on the Greater Antilles by the small endemic species *M. blainvillii,* which also is known by a single lower mandible from a pre-Columbian cave deposit on Exuma Island in the Bahamas (Koopman, 1951:229). For further information regarding distribution, see species accounts beyond and figures 36 and 40.

Description.—Bats of the genus *Mormoops* range in size from small to large; *Mormoops blainvillii* from Cuba being the smallest representative of the genus and *Mormoops megalophylla* from Ecuador being the largest. Externally, *Mormoops* is easily distinguished from *Pteronotus* as follows: long, lax pelage; short and rounded ears that are strongly connected dorsally on the rostrum by two, conspicuous ridges; lower edge of pinna confluent with lower lip; ornamentation of lower lip complex, with many intricate folds and scallops, forming a shield-like plate (covered with many wart-like tubercles) in front of a narrow central tubercle; a secondary transverse ridge below lower lip further complicates the structure (when opened, the mouth forms a funnel-shaped orifice that, coupled with the long, stiff hairs located at the sides of the mouth, probably form an efficient apparatus for catching insects); labio-nasal plate complex with nostrils surrounded by separate pads and separated by a long, wart-like ridge; margin above and between nostrils with several long, irregularly-shaped tubercles (Fig. 11F); tragus complex, secondary fold prominent, pubescence restricted to several long hairs and numerous short, bristles on the cranial edge (Fig. 10, G-H); wing membranes attach relatively high on sides of body but somewhat lower than in *Pteronotus*; uropatagium and wing membrane attach to ankle by way of a short ligament that is not bound to the tibia.

The cranium of *Mormoops* is unusual in shape, in that the rostrum is strongly upturned, and the forehead rises so abruptly over the braincase that it is almost at a right angle to the rostral part of the skull (Fig. 37). Additional features of the cranium of *Mormoops* are: zygomatic arches angled as a result of rostro-braincase flexion; mastoid flanges nearly absent and mastoid bone little more than short spicules above and behind auditory bullae; parietals noticeably inflated in area that encases cerebelli; infraorbital foramen located at maxillary root of zygomatic arch (Fig. 18); incisive foramina extremely large; basioccipital region relatively broad between bullae and basisphenoid with cup-like depression, into which the *M. longus capitus* inserts.

The molars are typically dilambdo-

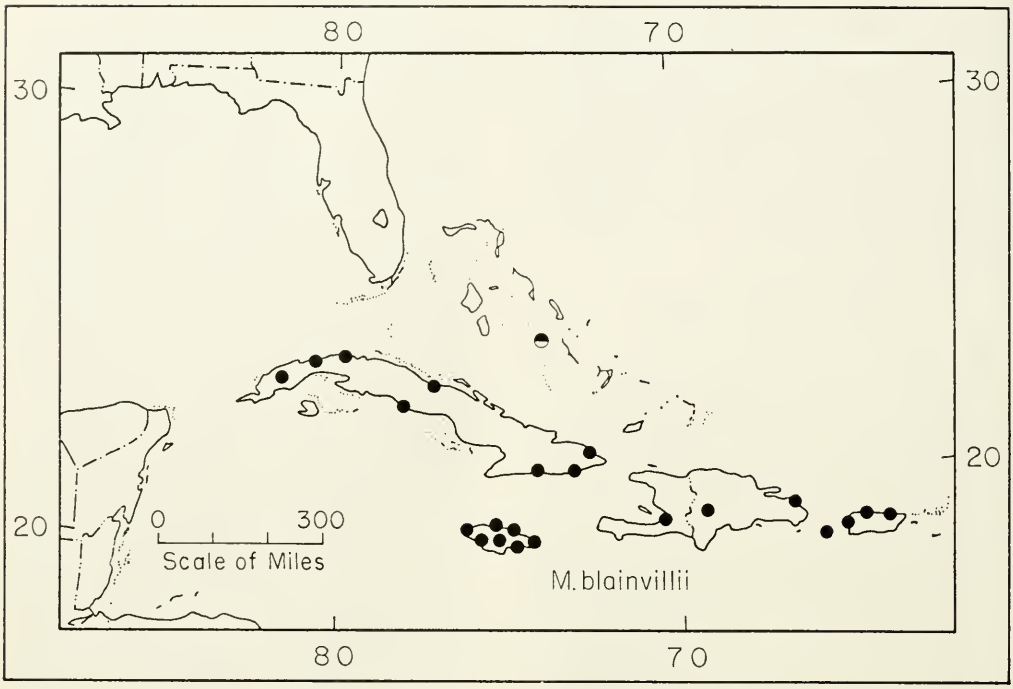


FIGURE 36. Distribution of *Mormoops blainvillii.*

dont and there are striking diastemas in the upper toothrow between the outer incisor and the canine as well as between the first and second premolars; upper incisors thin and blade-like, heel on inner pair completely absent; upper canine deeply grooved on the anteromedial surfaces; lower incisors small and delicate, all four are trilobed, heels absent; second lower premolar long and narrow; posterior portion of ramus markedly curved also reflecting cranial flexion.

Remarks.—Bats of this genus are the most specialized in the family Mormoopidae. Various morphological peculiarities seem to have been canalized toward the adaptation of these bats to a swift-flying insectivorous niche. The structure of the humerus, long, relatively narrow wings, funnel-shaped mouth, and enlarged cerebelli are among a few of these specializations. Inasmuch as these and other features are not nearly so markedly developed in the genus *Pteronotus,* it seems reasonable to suspect that *Mormoops* segregated from the mainline of mormoopid evolution at a relatively early stage.

I herein follow Opinion 462 (16 [pt. 1]:1-12, April 2, 1957) of the International Commission on Zoological Nomenclature in applying the generic name *Mormoops* in preference to *Aello,* which has eight pages of priority.

Mormoops blainvillii Leach

ANTILLEAN GHOST-FACED BAT

Mormoops Blainvillii Leach, 1821, Trans. Linn. Soc., 13:77.

Aëllo Cuvieri Leach, 1821, Trans. Linn. Soc., 13:71. Type locality unknown, herein presumed to be Jamaica. Holotype, adult, sex unknown, skin an skull, BM (no registration number); presented by W. Bullock to D. Brooke's Museum.

L[obostoma]. cinnamomeum Gundlach, 1840, Arch. Naturgesch., 6:357. Type locality, Cafetal St. [San] Antonio El Fundador, Matanzas, Cuba; present disposition of holotype unknown.

Holotype.—Not certainly located, presumably in the British Museum (Na-

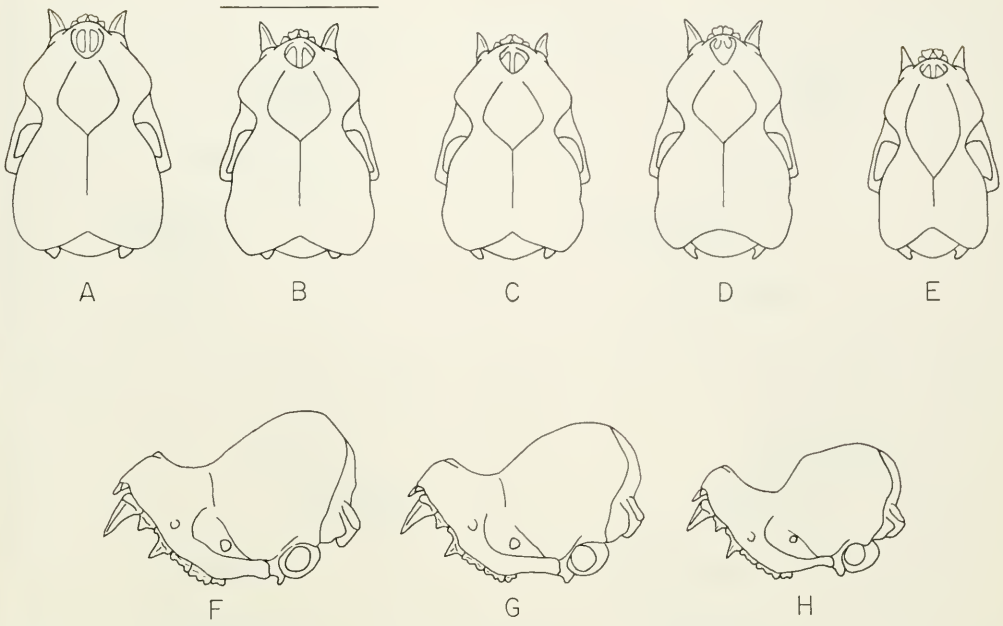


FIGURE 37. Dorsal and profile views of skulls of *Mormoops megalophylla carteri* (A and F, La Paz, Ecuador), *M. m. tumidiceps* (B, near Cartagena, Colombia), *M. m. intermedia* (C, Curaçao), *M. m. megalophylla* (D and G, Purificación, Jalisco), *M. blainvillii* (E and H, Cuba). All specimens are adult males; horizontal line above B is 10 mm in length.

tural History); from Jamaica; presented by Dom. Lewis to D. Brooke's Museum.

Distribution.—Greater Antilles, including Mona Island between Hispaniola and Puerto Rico. Koopman (1951: 229) reported a single mandible found in a pre-Colombian cave deposit on Exuma Island in the Bahamas (Fig. 36).

Description.—Smallest species of the genus *Mormoops*, forearm usually less than 41 (see measurements). Rostrum extremely upturned (as described above) and relatively narrow; braincase globular and with frontal region somewhat inflated, which emphasizes the abrupt rise of the forehead (Fig. 37); basioccipital and basisphenoid narrow, with a wide trough-like depression that lacks a longitudinal, medial septum; ears rounded, but with an inconspicuous dorsal portion that is short and pointed; large fleshy papilla on each side of upper lip; anterior folds of lower lip squared and plate-like; tragus complex and with secondary fold comprising largest part of the structure; short, lanceolate flap above secondary fold (Fig. 10H); tail and hind limbs long in proportion to length of body.

Most of the specimens of this species examined in this study were preserved in alcohol thereby limiting an evaluation of color. In a series of December- and January-taken males from Oxford Cave, Jamaica, the pelage was deep cinnamon brown dorsally and only slightly paler ventrally. The bases of individual hairs are pale reddish in color. It is here presumed that these individuals were in fresh pelage; paler and somewhat browner individuals have been taken at other times in the year.

Measurements.—Selected external and cranial measurements (average, with extremes in parentheses, plus or minus two standard errors of the mean) of nine adult males from Cuba, eight from Jamaica, six from Hispaniola, and 11 from Puerto Rico (sample size in

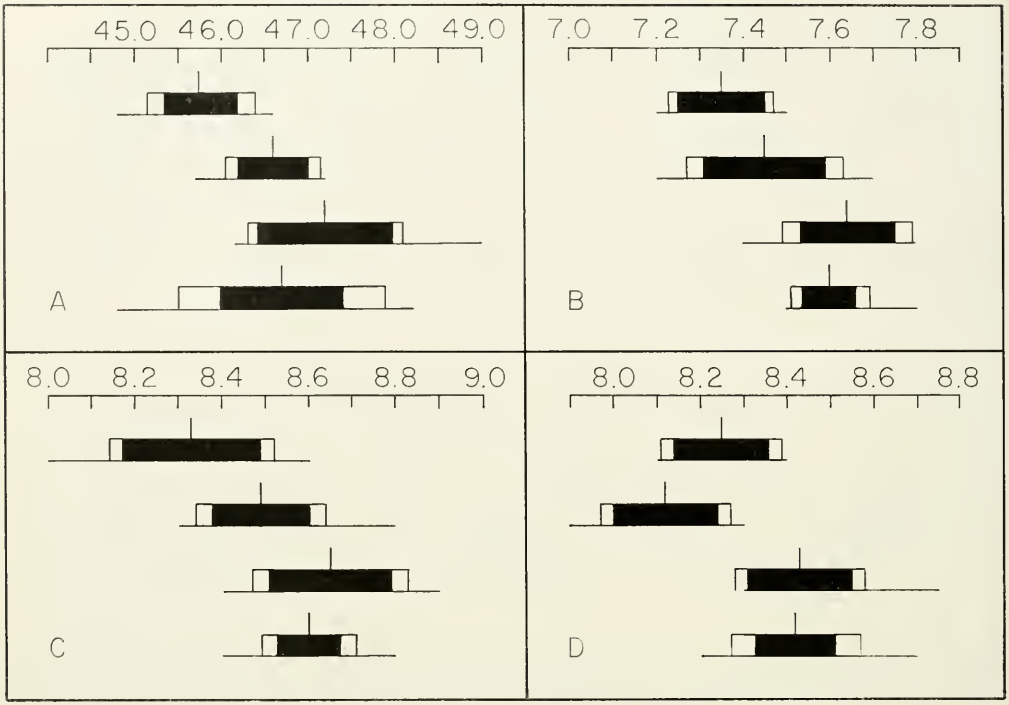


FIGURE 38. Dice-squares illustrating geographic variation of *Mormoops blainvillii* from the Greater Antillean islands of Cuba, Jamaica, Hispaniola, and Puerto Rico (top to bottom). The measurements illustrated (in mm) are: A, length of forearm; B, length of maxillary toothrow; C, zygomatic breadth; D, depth of cranium. See figure 26 for explanation of symbols.

brackets if different), respectively, are as follows: length of forearm, 45.8 (44.8-46.6) ± 0.39, 46.6 (45.7-47.2) ± 0.40, 47.2 (46.2-49.0) ± 0.80, 46.7 (44.8-48.2) ± 0.72; zygomatic breadth, 8.3 (8.0-8.6) ± 0.16 [6], 8.5 (8.3-8.8) ± 0.11, 8.6 (8.4-8.9) ± 0.14, 8.6 (8.4-8.8) ± 0.07 [10]; rostral breadth, 6.5 (6.3-6.6) ± 0.13 [6], 6.5 (6.1-6.7) ± 0.74, 6.7 (6.5-6.9) ± 0.11, 6.8 (6.6-7.0) ± 0.07; length of maxillary toothrow, 7.3 (7.2-7.5) ± 0.10 [6], 7.4 (7.2-7.7) ± 0.13, 7.6 (7.4-7.8) ± 0.11 [7], 7.6 (7.5-7.8) ± 0.06; condylobasal length, 12.8 (12.6-13.0) ± 0.14 [6], 13.0 (12.8-13.4) ± 0.17, 13.3 (12.8-13.7) ± 0.27, 13.3 (13.0-13.5) ± 0.09 [10]; depth of cranium, 8.2 (8.1-8.4) ± 0.11 [6], 8.1 (7.9-8.3) ± 0.11, 8.4 (8.3-8.7) ± 0.13, 8.4 (8.2-8.7) ± 0.09 [10]. No reliable standard external measurements are available.

Relationships.—Bats of this species are clearly related to the mainland species *Mormoops megalophylla*, but the Antillean bats evidently have been separated from the mainland species for quite some time. *Mormoops blainvillii*, along with *P. fuliginosus* and *macleayii*, probably represents a relatively old mormoopid lineage on the Greater Antilles.

Geographic variation.—Analysis of geographic variation of this species has been somewhat limited owing to a paucity of material. Two subspecies, *M. b. blainvillii* and *M. b. cinnamomeum* (= *M. b. cuvieri* Hall and Kelson, 1959:95), have been recognized in the past, based primarily on the shape of the first upper premolar. This character, however, is variable and appears to be of little taxonomic importance. The results of my analysis indicate a more or less continuous cline from Cuba to

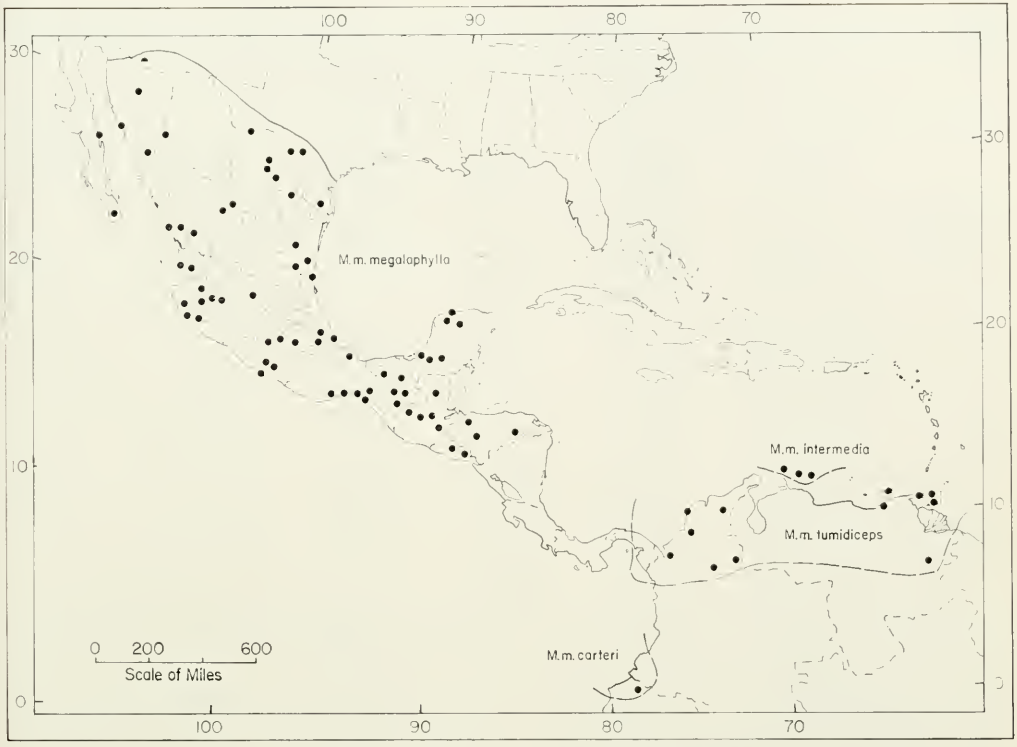


FIGURE 39. Distribution of *Mormoops megalophylla*.

Puerto Rico with a slight break or step between Jamaica and Hispaniola (Fig. 38). Cuban bats are the smallest in overall size and those from Hispaniola frequently are the largest, with representatives from Puerto Rico equal to, or slightly smaller than, those from Hispaniola. The greatest differences observed between bats from Cuba and Jamaica on the one hand and those from Hispaniola and Puerto Rico on the other, were in depth of cranium and length of maxillary toothrow (Fig. 38). Individuals of the Jamaican population were usually intermediate in size between Cuban and Hispaniolan bats. In view of the relatively continuous clinal variation between these populations, I do not feel that recognition of subspecies is justified and regard *M. blainvillii* as monotypic. In any event, the Cuban and Jamaican populations do not warrant recognition as two separate races, as supposed in the past.

If at a later date, additional evidence should dictate the necessity of recognizing bats from Hispaniola and Puerto Rico as subspecifically distinct from the populations on Cuba and Jamaica, there will be a nomenclatural problem involving the name *Aello cuvieri* because its type locality is unknown. Concerning this matter, Hall and Kelson (1959: 95) stated: "type from unknown locality, here assumed to be Cuba, but possibly Jamaica." Both Dobson (1878: 456) and Rehn (1902:162) presumed that the specimen on which the name *cuvieri* was based originated from Jamaica, which I feel is reasonable, and I recommend that the type locality be restricted to that island.

Specimens examined (125).—CUBA. *Habana:* 4 mi San José de Las Lajas, 1 (AMNH). *Oriente:* Baracoa, 6 (USNM); San Carlos Estate, Guantanamo, 1 (USNM); Santiago de Cuba, 1 (AMNH); *Caney,* 4 (ROM); *Cueva de la Cantera, Caney,* 1 (ROM); *Cueva de Las Majaes, Siboney,* 3 (2 AMNH, 1 ROM).

TABLE 5. Selected external and cranial measurements of several populations of *Mormoops megalophylla*. Each measurement is represented by the observed range, below which is the mean, plus or minus two standard errors of the mean; superscript numbers indicate sample size if different from that given in left-hand column. See text for the localities.

Locality	N	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
			Mormoops megalophylla megalophylla				
1	30	54.9±0.28[29]	9.6±0.05	7.4±0.03	8.0±0.04	14.3±0.07	9.7±0.06
		(53.0–56.5)	(9.4–9.9)	(7.3–7.6)	(7.8–8.3)	(14.0–14.7)	(9.4–10.0)
2	12	54.6±0.58[15]	9.5±0.06	7.3±0.07	7.9±0.19	14.1±0.09	9.6±0.10
		(52.3–56.3)	(9.3–9.6)	(7.1–7.5)	(7.7–8.9)	(13.8–14.3)	(9.2–9.8)
3	5	54.9±0.77[4]	9.5±0.13	7.3±0.05	8.0±0.10	14.2±0.10	9.6±0.14
		(54.2–56.0)	(9.3–9.7)	(7.3–7.4)	(7.8–8.1)	(14.0–14.3)	(9.5–9.8)
4	6	54.5±0.90	9.5±0.13	7.3±0.04	7.9±0.12	14.1±0.12[5]	9.6±0.16[6]
		(52.9–56.2)	(9.3–9.7)	(7.3–7.4)	(7.7–8.0)	(14.0–14.3)	(9.3–9.8)
5	4	53.1±0.90	9.3±0.05	7.0±0.13	7.8±0.08	13.8±0.21	9.6±0.08
		(52.4–54.4)	(9.3–9.4)	(6.9–7.2)	(7.7–7.9)	(13.6–14.0)	(9.5–9.7)
6	27	54.5±0.42	9.4±0.06	7.3±0.05	7.9±0.04	14.1±0.07	9.6±0.08
		(51.0–56.8)	(9.1–9.7)	(7.0–7.5)	(7.8–8.1)	(13.7–14.5)	(9.3–10.0)
7	18	54.4±0.40	9.5±0.09[12]	7.3±0.06	7.8±0.06	14.0±0.09[13]	9.6±0.07[13]
		(52.6–55.4)	(9.2–9.7)	(7.1–7.5)	(7.6–8.0)	(13.7–14.2)	(9.5–9.9)
8	39	54.3±0.34	9.4±0.06[24]	7.3±0.04	7.9±0.04	14.0±0.07[35]	9.6±0.07[35]
		(51.6–56.4)	(9.0–9.7)	(7.1–7.7)	(7.6–8.2)	(13.6–14.4)	(9.2–10.0)
9	19	54.1±0.60[20]	9.4±0.08	7.3±0.08	8.0±0.07	14.1±0.12[17]	9.6±0.05[16]
		(51.8–57.2)	(9.1–9.9)	(7.0–7.6)	(7.7–8.2)	(13.6–14.6)	(9.4–9.7)
10	40	55.5±0.25[47]	9.5±0.04	7.4±0.04	7.9±0.04	14.1±0.06[39]	9.7±0.04[39]
		(53.7–57.2)	(9.3–9.9)	(7.1–7.8)	(7.5–8.1)	(13.8–14.5)	(9.4–9.9)
11	24	55.0±0.36[23]	9.6±0.08[22]	7.4±0.05	8.0±0.04	14.2±0.10	9.8±0.09[23]
		(52.5–56.8)	(9.3–10.1)	(7.2–7.7)	(7.8–8.2)	(13.6–14.6)	(9.1–10.1)
12	4	53.6±0.48[11]	9.5±0.08	7.5±0.13	7.9±0.13	13.8±0.21	9.6±0.10
		(52.3–54.9)	(9.4–9.6)	(7.3–7.6)	(7.8–8.1)	(13.6–14.1)	(9.5–9.7)
13	32	54.1±0.37	9.5±0.06	7.5±0.04	8.0±0.04	14.0±0.11	9.7±0.05
		(52.0–57.3)	(9.1–9.8)	(7.3–7.8)	(7.7–8.3)	(13.6–14.8)	(9.3–10.0)
14	26	55.8±0.59	9.7±0.08[25]	7.6±0.06	8.1±0.05	14.4±0.15	9.8±0.09
		(53.0–58.8)	(9.2–10.1)	(7.2–7.8)	(7.9–8.3)	(13.6–14.9)	(9.2–10.1)
			Mormoops megalophylla intermedia				
17	3	54.1±0.10[4]	9.4±0.07	7.7±0.18	7.9±0.22[4]	13.8±0.24	10.0±0.20
		(54.0–54.2)	(9.4–9.5)	(7.5–7.8)	(7.6–8.1)	(13.6–14.0)	(9.8–10.1)
18	16	52.0±0.20[70]	9.3±0.10[15]	7.4±0.05	7.7±0.07	13.6±0.14[15]	9.7±0.03
		(49.8–53.8)	(9.0–9.7)	(7.2–7.6)	(7.5–7.9)	(13.3–14.4)	(9.4–10.4)
19	2	50.3, 53.4	9.2, 9.6	7.5, 7.6	7.5, 7.6	13.1, 13.5	9.3, 9.5

TABLE 5. (Continued)

Locality	N	Length of Forearm	Zygomatic Breadth	Rostral Breadth	Length of Maxillary Toothrow	Condylobasal Length	Depth of Cranium
			Mormoops megalophylla tumidiceps				
15	5	55.9±0.29[35]	9.5±0.24	7.5±0.17	7.9±0.13	13.9±0.27	9.8±0.21
		(52.6–58.8)	(9.3–9.8)	(7.2–7.7)	(7.7–8.1)	(13.6–14.3)	(9.5–10.1)
16	4	56.0±1.13	9.7±0.21	7.6±0.25	8.0±0.10	14.2±0.28	10.2±0.13
		(54.6–57.3)	(9.5–10.0)	(7.3–7.9)	(7.9–8.1)	(13.9–14.5)	(10.1–10.4)
20	23	56.0±0.45	9.7±0.06[19]	7.7±0.07	7.9±0.07	14.1±0.09[23]	10.1±0.07
		(53.7–57.3)	(9.5–10.0)	(7.3–8.0)	(7.7–8.2)	(13.8–14.5)	(9.8–10.4)
21	13	56.4±1.01	9.6±0.10	7.7±0.08[12]	7.9±0.08	14.1±0.13	10.1±0.11[12]
		(53.0–59.8)	(9.3–9.9)	(7.5–7.9)	(7.8–8.2)	(13.7–14.5)	(9.7–10.4)
			Mormoops megalophylla carteri				
22	21	58.8±0.48[19]	10.1±0.08	7.9±0.12	8.3±0.06	14.7±0.10	10.3±0.06
		(56.6–60.6)	(9.8–10.3)	(7.0–8.3)	(8.1–8.7)	(14.4–15.1)	(10.0–10.6)

Pinar del Río: Cueva del Indio, San Vicente, 15 (AMNH); *Cueva del Río, San Vicente,* 1 (ROM); *San Vicente,* 2 (ASC); Cueva de William Palmer, Guanajay, 3 (TCWC). *Las Villas:* Cueva Grande, Yaguajay, 4 (FMNH); Cueva de los Masones, Trinidad, 2 (ASC). JAMAICA. *Hanover:* Lucea, 1 (AMNH). *Portland:* Port Antonio, 1 (USNM). *St. Andrew:* Kingston, 1 (USNM). *St. Ann:* Dry Harbor, 2 (AMNH); Moneague, 1 (USNM). *St. Catherine:* St. Clair Cave, 9 (2 LACM, 5 ROM, 2 USNM). *St. Elizabeth:* Oxford Cave, 9 (AMNH). HAITI. Diquini, 1 (MCZ). DOMINICAN REPUBLIC. *Altagracia:* Cueva Las Lagunas de Nisibon, 1 (FMNH). *San Juan:* Rancho La Guardia, 4 (AMNH). PUERTO RICO. Mona Island, 8 (USNM); Mayaguez, 1 (USNM); Los Chorros Cave, near Arecibo, 37 (ROM); Cueva Trujillo Alto, 5 (AMNH).

Additional marginal record.—Exuma Island, Koopman (1951:229).

Mormoops megalophylla Peters

PETERS' GHOST-FACED BAT

(Synonymy under subspecies)

Distribution.—From southwestern Texas and southern Arizona, southward through México (including southern Baja California, the Mexican Plateau, and Yucatan Peninsula) into Central America as far as eastern Honduras and El Salvador. This species has not yet been recorded from Nicaragua, Costa Rica, or Panamá. In South America, *M. megalophylla* is known from several widely separated localities along the Caribbean coast of Colombia, Venezuela, Trinidad, and the Dutch West Indies, and also is known from the arid upper Patía Valley in northern Ecuador (Fig. 39).

Description.—Largest species of the genus *Mormoops,* forearm usually more than 50. Rostrum extremely upturned and broad; braincase, viewed in profile, squared and somewhat flattened dorsally or pyramidal lacking noticeable flattening (Fig. 37); forehead arises abruptly from rostrum; basioccipital and basisphenoid broad and trough-like between auditory bullae, with a prominent longitudinal, medial septum; ears rounded and strongly connected by two high bands that fuse on top of rostrum; tragus complex, with an extremely prominent secondary fold (Fig. 10G); labionasal plate also complex, each nostril surrounded by a separate pad; margin above and between nostrils with several wart-like tubercules; long and prominent ridge separates each nostril (Fig. 11F); dorsal pelage long and lax, with four zones of coloration on each hair.

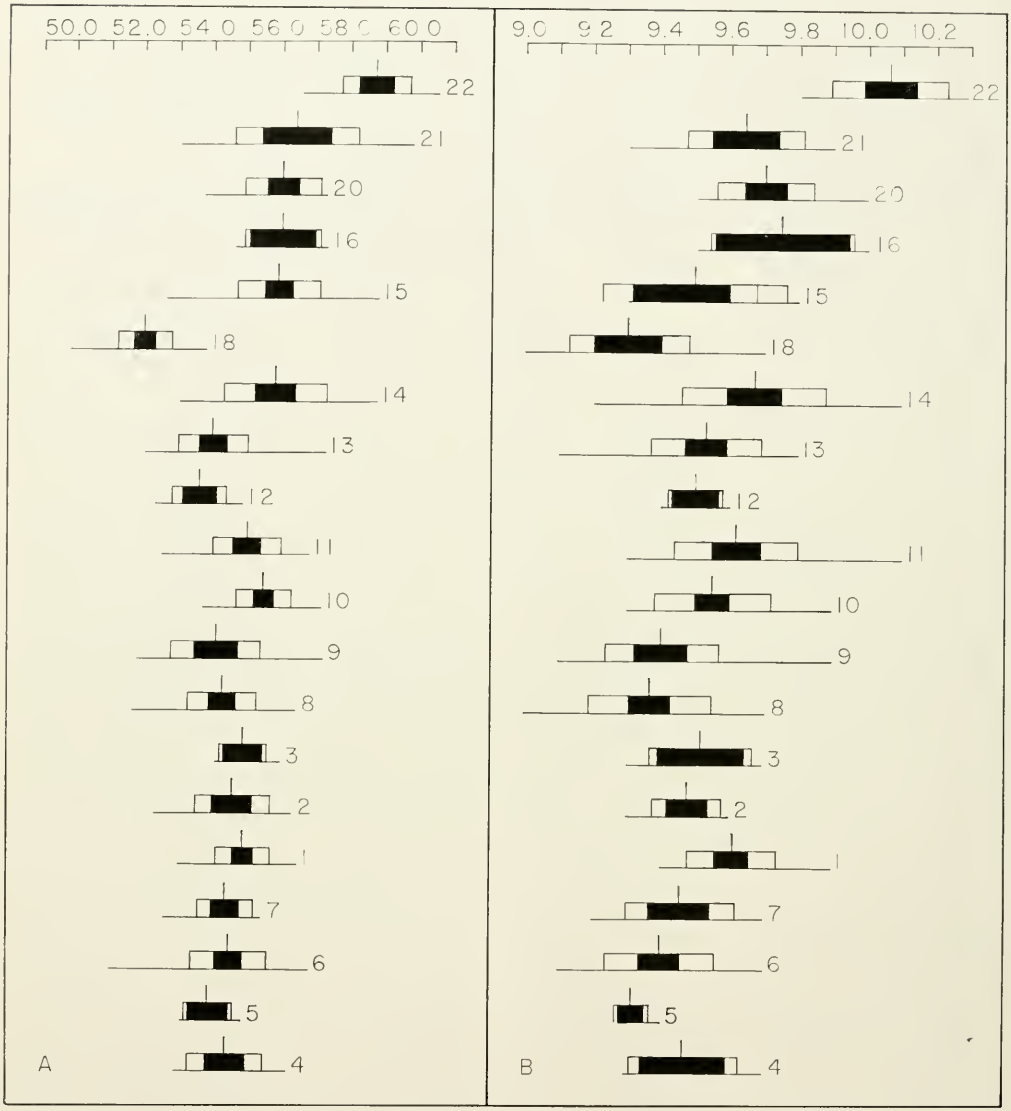


FIGURE 40. Dice-squares illustrating geographic variation of *Mormoops megalophylla* from selected mainland localities (see text for key to localities). The measurements illustrated (in mm) are: A, length of forearm; B, zygomatic breadth. See figure 26 for explanation of symbols.

Relationships.—See account of *M. blainvillii.*

Geographic variation.—My analysis indicates that there is a relatively small amount of geographic variation in North American populations (Table 5 and Fig. 40, localities 1-14). There appears to be a considerable amount of variation within samples and only a gradual increase in overall size in the extreme southern (Honduras) part of the range.

Although a rather large number of specimens of *M. megalophylla* were examined from South America, these were from relatively few and widely separated localities. South American representatives of this species generally average larger than those from México and northern Middle America (Table 5 and Fig. 40, localities 17-22). In addi-

tion to somewhat larger size, there are several other features that seem to characterize all South American populations. One of these concerns the shape of the braincase and particularly the outline of the forehead, viewed in profile. In the Mexican representatives of the species, the forehead rises abruptly, but flattens gradually on top of the braincase. This flattening is not so apparent in the South American bats (Fig. 37) and, in fact, the forehead seems to include both frontal and parietal regions. There are no other striking cranial differences.

Externally several noteworthy characteristics further distinguish South American bats from North American representatives. The color of fresh pelage in these bats is a deep cinnamon red with an iridescent, purplish frost over the back and rump. Ventrally, the pelage is pinkish or reddish in color. These colors vary somewhat depending on geographic location, age of the pelage, or degree of bleaching. The most striking feature of the pelage of the South American representatives of *M. megalophylla* is the development of a white or pinkish, fan-shaped "cape" over the shoulders, formed by relatively long stiff hairs. This cape and the rich cinnamon coloration are absent in North American bats of this species. I do not believe these features represent specific differences between North and South American populations, although the observed geographic variation indicates somewhat greater subspecific differences than in other polytypic species of the family and possibly represents incipient speciation. It seems likely that these distinct geographic units were formed by spatial separation of a formerly widespread population in Pleistocene times, resulting in the subsequent isolation of North and South American segments of the species. In view of the relatively concentrated collecting efforts in the past decade or so in southern Middle America and the failure to obtain *M. megalophylla* there, the present distributional gap in this region is real. I assume that any reproductive isolation that may have developed during spatial isolation has not yet been tested, and I therefore elect to regard the South American populations as a distinctive subspecies group rather than as a distinct species.

The general pattern of geographic variation along the Caribbean coast of South America is one of gradual increase in overall size to the eastward. However, in the Dutch West Indies (localities 17-19), bats are smaller and paler than those on the adjacent mainland and are subspecifically distinct; the extreme of this trend being seen in specimens from the islands of Curaçao and Bonaire. A large series from the upper Patía Valley of Ecuador also constitutes a morphologically and geographically distinct population, which is herein given subspecific recognition. Bats from this region seem to be isolated on the arid Pacific versant of the Andes and are the largest representatives of the species.

Key to localities used in statistical analysis of geographic variation.—1, Concon, Uvalde Co., Texas; 2, northern Coahuila; 3, Tamaulipas; 4, Sonora; 5, Mulegé, Baja California; 6, southern Sinaloa; 7, vicinity of Amatlán, Nayarit; 8, vicinity of Ocotlán and Jamay, Jalisco; 9, Colima; 10, 1 mi E Raboso, Puebla; 11, southwestern Guerrero; 12, Campeche; 13, Lanquin Cave, Guatemala; 14, vicinity of Divisadero, El Salvador; 15, Cartegena, Colombia; 16, San Gil, Santander, Colombia; 17, Aruba; 18, Curaçao; 19, Bonaire; 20, vicinity of Guiria, Venezuela; 21, Trinidad; 22, La Paz, Ecuador.

Mormoops megalophylla megalophylla Peters

Mormops megalophylla Peters, 1864, Monatsb. preuss. Akad. Wiss., Berlin, p. 381.

Mormoops megalophylla senicula Rehn, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54:169, 11 June. Type locality, Fort Clark, Kinney Co., Texas. Holotype, adult female, skin and skull, USNM 84801; obtained by Dr. E. A. Mearns; original no. 4273.

Mormoops megalophylla rufescens Davis and Carter, 1962, Southwestern Nat., 7:65, 1 June. Type locality, 5 mi W Alamos, So-

nora, México. Holotype, adult male, skin and skull, LACM 9978; obtained by Kenneth E. Stager; original no. 1652.

Holotype.—Adult female, preserved in alcohol, skull removed, Zoologisches Museum Berlin no. 2826; type locality, Parrás, Coahuila, México (see remarks below); obtained by Schneider.

Distribution.—From southwestern Texas and southern Arizona, southward throughout México into Central America as far as eastern Honduras and El Salvador (Fig. 39).

Description.—Size small, both cranially and externally, for a mainland race of the species. Standard external measurements (average, extremes in parentheses) for 18 males and 13 females, respectively, from 3.5 mi S and 2.5 mi E Ocotlán, 500 ft, Jalisco, are as follows: total length, 88.9 (85.0-97.0), 90.9 (87.0-95.0); length of tail vertebrae, 24.9 (22.0-28.0), 25.1 (23.0-27.0); length of hind foot, 13.0 (12.0-14.0), 13.0 (13.0); length of ear from notch, 14.3 (13.0-15.0), 14.5 (14.0-15.0). See table 5 (localities 1-14), for additional selected external and cranial measurements.

In general, fresh pelage of this subspecies is brownish to pale brown (Prout's Brown to Snuff Brown) dorsally. A large series taken on 13 August near Raboso, Puebla, was composed of individuals that were in various stages of molt. Generally, old pelage of these bats was reddish brown, whereas fresh pelage was dark brown (Prout's Brown). The four zones of color of individual hairs from the back are, from base to tip, dark brown, pale brown to tannish, dark brown, and blackish brown. Individuals from Texas and northern México, and from northern Middle America, tend to be slightly darker than specimens from the intervening areas; however, a great deal of variation was observed in the samples examined. The specimens that Davis and Carter (1962) assigned to *M. m. rufescens* are reddish brown. The majority of these were collected at a time of year (December to August) when the pelage is usually reddish in color. Five adult males, caught on 28 July near Santa Lucía, Sinaloa, were actively molting from a reddish brown pelage to a darker, brownish gray pelage, which seems to indicate that the reddish color heretofore thought to be distinctive of *M. m. rufescens* actually represents seasonal variation.

Comparisons.—*Mormoops megalophylla megalophylla* is easily distinguished from South American subspecies by the absence of a fan-shaped "cape" over the shoulder region that is formed by relatively long, stiff hairs, and the somewhat flattened forehead as viewed from the side (Fig. 37). Except for the insular race *M. m. intermedia*, *M. m. megalophylla* is smaller in size, both cranially and externally than other subspecies (Table 5).

Remarks.—In the original description, Peters (1864) did not mention a precise type locality in México. In an earlier paper, he (1856) supposed these bats were from Cuba and referred to them as "*M. blainvillii.*" Rehn (1902: 167) compared three specimens of *M. megalophylla* (two from Mérida, Yucatán, and one from San Juan Bautista, Tabasco) with Peters' (1856: pl. 1, figs. 1-5) illustrations and concluded that the type locality should be regarded as southern México. Dilford C. Carter recently examined Peters' holotype of *M. megalophylla* in Berlin and noted that the locality "Parras, Mexico," in Peters' own handwriting, was associated with this specimen. In view of these circumstances, it seems appropriate to regard the type locality of *megalophylla* as the well-known collecting site, Parrás, Coahuila.

Three subspecific names have been applied to North American representatives of the species *megalophylla*. The name *senicula* was based primarily on size and shape of the second upper premolar, a characteristic found to be variable by Villa and Jiménez (1960: 503). This same variation was detected

by Davis and Carter (1962:65) who followed Villa and Jiménez in regarding *senicula* as a junior synonym of *M. m. megalophylla*. I agree with these authors in this matter.

Davis and Carter (1962:65-67) reviewed the North American representatives of this species and concluded that, on the basis of color, there were two geographic groups; the one from northwestern México they named *M. m. rufescens*. Aside from the alleged reddish or cinnamon color of the pelage, these authors further diagnosed *rufescens* as having a short forearm (about 54) and a short, narrow skull. Bats from northwestern México do average slightly smaller than those from the northeastern and southern parts of the country, as noted by Davis and Carter, but the differences are so slight that, in the absence of an effective barrier, subspecific recognition of this population does not seem to be warranted. Specimens in a sample from Mulegé, Baja California, are somewhat smaller than other Mexican specimens, even those from the adjacent mainland, and additional material from this little-studied region may reveal that subspecific recognition is warranted for these peninsular bats.

The few specimens examined from the northern part of the Yucatan Peninsula average smaller than those from Campeche and other nearby regions. Also, as mentioned previously, bats from Honduras and El Salvador are slightly larger than individuals from further northward. An accurate appraisal of these trends will not be possible until the relationships between North American and South American races are better understood.

Specimens examined (787).—TEXAS. *Brewster County:* Oak Creek, Chisos Mts., 5000 ft, 2 (TCWC). *Hidalgo County:* Edinburg, 1 (TCWC). *Kinney County:* Fort Clark, 1 (USNM). *Medina County:* Valdina Farms sink hole, 3 (LACM); *Nye Cave,* 1 (LACM). *Uvalde County: Concon,* 11 (3 AMNH, 2 CAS, 6 USNM); *Fria Cave, Concon,* 36 (LACM); *9 mi W Sabinal,* 2 (USNM). MÉXICO. *Baja California:* 0.25 mi S Mulegé, 100 ft, 14 (MVZ); 3 km S San Antonio, 1 (KU). *Campeche:* 1 km N, 13 km W Escárcega, 65 m, 2 (KU); *12 km W Escárcega,* 4 (KU); 7 km N, 51 km E Escárcega, 1 (KU); *18 km S, 65 km E Escárcega,* 6 (KU); *La Tuxpeña,* 1 (USNM); 105 km E Escárcega, 1 (KU). *Chiapas:* 5 km S Palenque, 1 (ENCB); 3 mi E Cintalapa, 1700 ft, 1 (TCWC); 4.5 mi W San Cristóbal, 4 (UMMZ); La Soledad, approx. 16 mi NE Las Margaritas, 3600 ft, 1 (LACM); 5 mi N Arriaga, 800 ft, 2 (TCWC); Zapaluta, 5700 ft, 1 (TCWC); *1 mi S Zapaluta, 5700 ft,* 1 (TCWC); *2 mi S Zapaluta, 5700 ft,* 1 (TCWC); *18 mi S La Trinitaria, 2800 ft,* 3 (TCWC); Cueva León, 4 km ENE San Lucas, 1 (TCWC). *Chihuahua:* Carimechi, Río Mayo, 3 (TCWC). *Coahuila:* Fortín, Rancho Las Margaritas, 3300 ft, 1 (KU); *Las Margaritas,* 5 (KU); Puerta Santana, 6 mi S, 3 mi W Hacienda La Mariposa, 2900 ft, 10 (KU); 6 mi E Hermanas, 1200 ft, 3 (KU); Cueva del Buen Abrigo, Noria no. 5 E Coyote, Torreon, 12 (IB). *Colima:* 7 mi W, 0.5 mi S Santiago, sea level, 20 (KU); *Playa de Oro, 8 km W, 2 km S Santiago,* 1 (KU); 8 mi SE Colima, 20 (LACM). *Durango:* La Cueva de España, 2 km S, 11 km W Nazareno, 400 ft, 5 (TCWC); 2 mi N Pueblo Nuevo 6000 ft, 1 (MSU). *Guanaguato:* No specific locality, 1 (USNM). *Guerrero:* Grutas de Cacahuamilpa, 27 (24 ENCB, 3 KU); Agua de Obispo, 37 km S Chilpancingo, 980 m, 2 (KU); *5 mi E Omilteme, 6200 ft,* 1 (USNM); Grutas de Juxlahuaca, 4 km NE Colotlipa, 1100 m, 12 (11 ENCB, 1 IB); 2 mi NW Acapulco, 50 ft, 15 (KU). *Jalisco:* 15 km W Ameca, 4200 ft, 2 (KU); Los Masos, 8 (6 AMNH, 2 FMNH); 18 km NW Purificación, 8 (KU); 16 mi NE Tamazula, 5000 ft, 2 (TCWC); 5 mi W Chapala, 5000 ft, 1 (KU); 3.5 mi S, 2.5 mi E Ocotlán, 5000 ft, 45 (41 KU, 4 MSU); 0.5 km N, 3 km W Jamay, 1650 m, 9 (IB). *Morelos:* Cueva del Salitre, 10 km NNW Tecumán, 36 (IB). *Nayarit:* San Blas, 7 (MVZ); *0.5 mi E San Blas, 10 ft,* 27 (KU); Rancho Palo, near Amatlán, 36 (35 AMNH, 1 FMNH). *Nuevo Leon:* Mina Jésus María, 10 km SSE Vallecito, 12 (IB). *Oaxaca:* 5 mi W Chiltepec, 2 (AMNH); 8 km NW Salina Cruz, 3 (ENCB); Tapanatepec, 2 (AMNH). *Puebla:* 1 mi E Raboso, 4350 ft, 54 (KU). *Sinaloa:* Mazatlán, 2 (USNM); Pánuco, 22 km NE Concordia, 25 (KU); *1 mi E Santa Lucía, 3650 ft,* 1 (KU); 1.5 km S Santa Lucía, 3200 ft, 5 (KU). *Sonora:* Cueva del Tigre, 14.9 mi SE Carbó, 7 (LACM); *20 mi SE Carbó, 2700 ft,* 1 (LACM); Rancho San José, 15 mi NW Guaymas, 2 (KU); La Aduana, 1 (LACM); *4 mi N Alamos, 1500 ft,* 2 (KU); 5 mi W Alamo, 6 (5 LACM, 1 AMNH). *Tabasco:* 5 mi SW Teapa, 1 (KU); *Arroyo del Solpho, Tapiajulapa,* 2 (AMNH); San Juan Bautista, 1 (USNM). *Tamaulipas:*

Rancho Santa Rosa, 25 km N, 13 km W Ciudad Victoria, 260 m, 1 (KU); Sierra de Tamaulipas, 16 mi W, 16 mi S Piedras, 1400 ft, 4 (KU); Cueva del Pachon, 3 (USNM); Tampico, 7 (USNM). *Veracruz:* Mirador, 27 (USNM); 4 km WNW Fortín, 3200 ft, 1 (KU); *Orizaba,* 5 (USNM); 6 km WSW Boca del Río, 10 ft, 1 (KU); 3 km E San Andrés Tuxtla, 1000 ft, 4 (KU). *Yucatán:* 10 mi W Progresso, 1 (LACM); Mérida, 2 (USNM); Cruta Balancanche, 5 km E Chichén Itzá, 1 (KU). GUATEMALA. *Alta Verapaz:* 3 km ENE San Cristóbal Verapaz, 1370 m, 3 (TCWC); Lanquin Cave, 1022 ft, 60 (KU); Piedra de Jalali, 4 km NE Cahabón, 1 (AMNH). *Chiquimula:* 20 km SSE Chiquimula, 550 m, 1 (TCWC); *Jocotán, near Chiquimula, 1350 ft,* 1 (KU). *Huehuetenango:* San Pedro Soloma, 2270 m, 1 (TCWC). *Petén:* 2 mi S Flores, 32 (AMNH); Laguna de Zotz, 1 (USNM). HONDURAS. *Comayagua:* Comayagua, 580 m, 1 (TCWC). *Olancho:* San José, Río Tinto, 340 m, 5 (TCWC). *Santa Barbara:* 2 km S San Nicolas, 660 m, 13 (TCWC). EL SALVADOR. *Cuscatlán:* 2 km W Suchitoto, 390 m, 1 (TCWC). *La Unión: Tabanco, 650 ft,* 4 (MVZ). *Morazán:* Encuentros Mine, 3 mi W Divisadero, 700 ft, 51 (MVZ); *San José Mine, approx. 1 mi W Divisadero,* 1 (MVZ).

Mormoops megalophylla intermedia Miller

Mormoops intermedia Miller, 1900, Proc. Biol. Soc. Washington, 13:160, 31 October.
Mormoops megalophylla intermedia Rehn, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54:170, 11 June.

Holotype.—Adult female, preserved in alcohol, skull not removed, USNM 102174; from cave at Hatto, north coast of Curaçao, Dutch West Indies, obtained on 29 April 1900; collector unknown.

Distribution.—Dutch West Indies (Fig. 39).

Description.—Smallest of the South American subspecies of the species, both cranially and externally (Table 5). Standard external measurements (average, with extremes in parentheses) for four males from Curaçao are as follows: total length, 78.0 (74.0-83.0); length of tail vertebrae, 19.5 (18.0-21.0); length of hind foot, 10.5 (9.0-12.0). Additional selected external and cranial measurements are given in table 5 (localities 17-19). In addition to overall small cranial size, the rostrum is short, the upper teeth are noticeably crowded, and the second lower premolar is extremely small as compared to the larger first and third lower premolars.

Nearly all of the specimens of this subspecies examined were preserved in alcohol and most were badly bleached. In general, the color of the pelage was pale brown. The hairs that form the "cape" over the shoulders are white. The cape is not particularly prominent on the holotype, but is prominent on other individuals that I examined.

Comparisons.—From *M. m. megalophylla* of the North American mainland, *M. m. intermedia* is distinguished by the presence of the fan-shaped shoulder cape and more steeply rising braincase (Fig. 37). From *M. m. tumidiceps* of the adjacent mainland, *M. m. intermedia* may be recognized by its smaller external and cranial size, as well as shorter rostrum, more crowded upper teeth, and relatively small second lower premolar. In both North American and South American mainland populations, the second lower premolars are not reduced, compared to the first and third, as it is in *M. m. intermedia.*

Remarks.—There is a noticeable trend to smaller overall size from Aruba to Bonaire in this insular subspecies. In general, bats from the continental island of Aruba are intermediate in size between those of the adjacent mainland and the islands of Curaçao and Bonaire (Table 5). As has been mentioned previously, suboptimal ecological factors as well as the small landmass of these islands probably have been important features in the differentiation of this insular race.

Specimens examined (110).—ARUBA. Quadirikiri Caves, 4 (AMNH); *Lago Oil Transport Co.,* 5 (AMNH); *5 mi E Seroe Colorado,* 14 (AMNH); *Ex-cave,* 4 (USNM). CURAÇAO. Round Cliff, 4 (AMNH); *Northwest end of island,* 7 (USNM); no specific locality, 70 (2 AMNH, 50 FMNH, 18 USNM). BONAIRE. Oeroesjan Blanco, Grot Colombia, near Barcadera, 2 (RMNH).

Mormoops megalophylla tumidiceps Miller

Mormoops tumidiceps Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54:403, 12 September.

Mormoops megalophylla tumidiceps—Goodwin and Greenhall, 1961, Bull. Amer. Mus. Nat. Hist., 122:225, 26 June.

Holotype.—Adult male, preserved in alcohol, skull removed, USNM 186443; from Point Gourde Caves, Trinidad, obtained in 1889 by Sir William Robinson.

Distribution.—Northern South America, primarily along Caribbean coast, but known also from several inland localities (Fig. 39).

Description.—Size moderately large, externally and cranially, among South American subspecies. Standard external measurements (average, with extremes in parentheses) for 18 males and three females, respectively, from Río Salado, 9 km N and 4 km E Guiria, Sucre, Venezuela, are as follows: total length, 95.8 (88.0-104.0), 97.0 (92.0-100.0); length of tail vertebrae, 27.7 (24.0-31.0), 26.0 (24.0-29.0); length of hind foot, 11.9 (10.0-13.0), 11.7 (11.0-12.0); length of ear from notch, 14.8 (13.0-16.0), 14.7 (14.0-15.0). See table 5 (localities 15-21) for additional selected external and cranial dimensions.

Specimens in fresh pelage are a deep cinnamon red dorsally, with an iridescent purplish frost. Hairs that form the cape are pale pink to rose pink in color. Ventrally, the pelage is pale pinkish to reddish.

Comparisons.—For comparisons with other South American subspecies, see the account of *M. m. intermedia* and the following account of a new subspecies from Perú.

Remarks.—Generally, overall variation in this subspecies is relatively small and similar in degree to that observed in *M. m. megalophylla*. Bats from Trinidad average slightly smaller in size than specimens from the vicinity of Guiria, Venezuela, on the Peninsula of Paria.

Specimens examined (106).—COLOMBIA. *Bolívar:* Cartagena, 12 (2 ROM, 10 USNM). *Guajira:* Nazaret, 2 (ROM). *Magdalena:* Valledupar, César, 2 (ROM). *Santander:* San Gil, 6 (4 FMNH, 2 ROM); Barichara, Macaregua, 1700 m, 11 (FMNH). *Sucre:* Tolu Viejo, 1 (ROM). VENEZUELA. *Bolívar:* Hato San José, 146 km S, 7 km E Ciudad Bolívar, 306 m, 1 (USNM). *Nueva Esparta:* Cueva Honda del Piache, SE of El Valle, 2 (RMNH). *Sucre:* Río Salado, 9 km N, 4 km E Guiria, 90 m, 25 (USNM); *Ensenada Cauranta, 7 km N, 5 km E Guiria, 1 m,* 10 (USNM). TRINIDAD. Port of Spain, 2 (AMNH); *Point Gourde Caves,* 1 (USNM); *St. Joseph,* 2 (AMNH); *Tunapuna,* 1 (AMNH); Mt. Tamana Caves, 24 (4 AMNH, 15 FMNH, 2 KU, 1 TCWC, 2 ROM); Las Cuevas, 4 (LACM).

Mormoops megalophylla carteri new subspecies

Holotype.—Adult male, skin and skull, TCWC 11643; from Gruta Rumichaca, 2 mi E La Paz, 8700 ft, Carchí Province, Ecuador; obtained by Dilford C. Carter on 5 July 1964, original no. 5142.

Distribution.—Known only from the type locality, but probably occurs along the arid Pacific coast to northern Perú and possibly in the dry intermontane Cauca Valley of the Colombian Andes (Fig. 36).

Description.—Size largest, externally and cranially, of the geographic races of *M. megalophylla* (Table 5, locality 22). Standard external measurements of the holotype followed by the average, with extremes in parentheses, of 16 males and 18 females, respectively, from the type locality are as folows: total length, 94.0, 98.1 (93.0-103.0), 98.6 (95.0-102.0); length of tail vertebrae, 25.0, 28.3 (23.0-31.0), 27.5 (25.0-30.0); length of hind foot, 11.0, 10.8 (10.0-13.0), 9.9 (9.0-11.0); length of ear from notch, 16.0, 15.2 (14.0-16.0), 15.4 (15.0-16.0). See table 5 for additional selected external and cranial measurements of type series. Selected external and cranial measurements of the holotype are as follows: length of forearm, 58.7; zygomatic breadth, 10.0; breadth of braincase, 9.3; mastoid breadth, 8.9; zygorostral length, 12.0; interorbital breadth,

5.5; rostral breadth, 8.1; length of maxillary toothrow, 8.2; length of mandibular toothrow, 9.2; condylobasal length, 14.8; depth of cranium, 10.2.

The pelage of the holotype is dark cinnamon brown dorsally, paler ventrally. Five other males from the type locality are olive-brown in color.

Comparisons.—From *M. m. tumidiceps*, this new subspecies may be distinguished by its larger cranial and external size—forearm averaging 58.0 or more and condylobasal length measuring 14.5 or more.

Remarks.—This population appears to represent another case of geographic isolation along the arid Pacific coast of South America. These bats probably reached the region of northwestern Ecuador through southward dispersal along the arid intermontane Cauca Valley of Colombia and northern Ecuador. In the upper part of this valley there is a relatively low pass over which bats could have gained access to the upper Patía Valley and thence the arid Pacific versant of Ecuador. This route seems to be the most reasonable, although it is conceivable that they also may have arrived in northwestern Perú by following the narrow corridor formed by the Pacific versant of the Andes in western Colombia and Ecuador. According to Haffer (1967a) and Chapman (1926), this region may have been dominated by xeric conditions during pre-Pleistocene times. However, the subsequent development of tropical forest in this region in the Pleistocene may have blocked this route of dispersal for non-forest species.

It is with great pleasure that I name this subspecies in honor of Dilford C. Carter, who not only made these and many other specimens available to me, but also has been most helpful in providing valuable information concerning holotypes housed in various European museums.

Specimens examined (47).—ECUADOR. *Carchí:* Gruta Rumichaca, 2 mi E La Paz, 8700 ft, 47 (46 TCWC, 1 KU).

ZOOGEOGRAPHY AND SPECIATION OF MORMOOPIDS

Primarily because of their ability to fly, bats have been excluded from many discussions concerning mammalian zoogeography, a paradox inasmuch as birds have been widely used in zoogeographic studies. Some features that relate to the evolution and speciation of the Mormoopidae are discussed below.

Greater Antilles

This region has been important in the evolution and differentiation of several mormoopid species. Of these, three *(Pteronotus fuliginosus, P. macleayii* and *Mormoops blainvillii)* are endemic, presumably having evolved as a result of isolation in the Antilles. Insular populations of another species *(Pteronotus parnellii)* have diverged from their mainland relatives to a greater or lesser degree at the subspecific level. All the species excepting *P. macleayii* have been recorded from all four islands of the Greater Antillean complex. None is known from any of the Lesser Antillean islands, although a mandible of *M. blainvillii* was reported from a pre-Colombian cave deposit on Exuma Island in the Bahamas (Koopman, 1951: 229).

The concept that bats could traverse wide sea barriers and thereby populate insular areas was popular in the early part of the Twentieth Century, as was the concept of land bridges to account for the West Indian dispersal of some land mammals (Simpson, 1956). G. M. Allen (1911:176) commented on the supposed flying capabilities of bats: "Indeed, the very fact that where bats are found in islands they have usually become more or less differentiated from their nearest neighbors, and this in a uniform and constant manner, is proof

that such fortuitous methods of distribution as have been claimed for these animals are largely inoperative." It is now conceded that bats ordinarily are capable of crossing only narrow water gaps without a great deal of difficulty and that they generally are restricted in the same way as other mammals by wide water barriers (Koopman, 1958, 1970).

Climatic and geologic events of late Tertiary and Quaternary times probably have been of paramount importance in the dispersal and evolution of bats, both in the Antilles and on the Neotropical mainland. Appreciable fluctuations in sea level caused a restriction or expansion of the landmass in these areas. In the case of the Greater Antilles, a drop in the water level would have resulted in a considerably narrower water gap than now exists between Jamaica and the Honduras-Nicaragua region of Middle America. In view of the absence of representatives of Greater Antillean mormoopids in the Lesser Antilles and the lack of evidence to support a route of dispersal for mormoopids from Florida to Cuba, I presume that mormoopids as well as some other groups of bats arrived in Jamaica by crossing from the Honduras-Nicaragua region, or possibly to Cuba from Yucatán.

Pteronotus fuliginosus and *macleayii* are closely related and both appear to be related to the mainland species *personatus*. In both Antillean species, Cuban individuals are markedly smaller than those from Jamaica and are herein referred to distinct subspecies. The development of racial differences between Cuban and Jamaican populations points to the relative effectiveness of the water barrier that separates these islands. On the other hand, representatives of *P. fuliginosus* from Jamaica, Hispaniola, and Puerto Rico exhibit only minor differences in what appears to be a continuum of geographic variation, evidently reflecting a close geographic relationship in the past among the three islands in question. Both *fuliginosus* and *macleayii* could have evolved in isolation on the Antilles from a single invasion of *personatus*-like bats, with subsequent sympatry, or they could be the result of two invasions, with speciation of the first immigrant stock completed prior to arrival of the second. In view of the greater similarities between these two species than between either of them and *personatus*, it is most likely that they resulted from a single invasion.

In *Mormoops blainvillii*, a somewhat larger bat (and presumably a better flier) than either *fuliginosus* or *macleayii*, there is relatively little geographic variation. There is, however, a slight indication of a pattern in this species that suggests separation of bats on Cuba from those on Hispaniola and Puerto Rico, with bats from Jamaica providing the intermediate link.

The degree to which the three endemic Antillean species have diverged morphologically and evolutionarily from their mainland relatives is considerably greater than that observed in *Pteronotus parnellii*, evidently a more recent (probably Pleistocene) immigrant to the Greater Antilles. The association of a dated time sequence with the invasion of the Antilles by mormoopids (and other chiropterans) is impossible in the absence of a fossil record. By general inference, time required for morphological (and genetic) differentiation decreases with taxonomic rank. Presumably, therefore, the time required for the evolution of the endemic Antillean phyllostomatid subfamily Phyllonycterinae was considerably longer than that required to evolve most or all of the endemic Antillean stenodermine genera, the differentiation of which may well have preceded that at the specific level seen in mormoopids. Bats that have only recently invaded the West Indies would be expected to exhibit relatively few morphological differences from parental mainland populations. This appears to be the case in *Pteronotus davyi*, the only mormoopid that has success-

fully invaded the Lesser Antilles (Fig. 31). However, such linear inferences should be clearly regarded as speculative owing to our present lack of information concerning modes of chiropteran evolution. At this stage, a reasonable estimate of the time of arrival of the three mormoopid species that are endemic in the Antilles might be middle to late Pliocene.

Pteronotus parnellii evidently arrived later in the Greater Antilles than did the three endemic species. *Pteronotus p. parnellii* (from Cuba and Jamaica) and *P. p. portoricensis* (Puerto Rico) clearly are only subspecifically distinct from mainland representatives of the species, and the differences between these two insular races are small. Had they been located on adjacent islands, I would not have retained *portoricensis* as a distinct subspecies. However, in view of the interposed distribution of the markedly distinct subspecies *P. p. pusillus* and *P. p. gonavensis* (from Hispaniola and La Gonave Island, respectively), I regard Puerto Rican bats as a distinct subspecies.

There are several possible explanations for the unique distribution of Antillean subspecies of *parnellii*. Perhaps they represent independent insular evolution from a single immigrant stock. Another possibility would be to assume two invasions of the region by *parnellii*, the first represented by *pusillus* (and *gonavensis*) and the second by the larger (and evidently related) *parnellii* and *portoricensis*. It is uncertain whether there is gene flow between Hispaniolan *pusillus* and the populations on Cuba, Jamaica, and Puerto Rico. If not, then serious consideration should be given to elevating *pusillus* (with *gonavensis* as a distinct subspecies) to full specific rank, and placing *portoricensis* in synonymy under *P. p. parnellii*.

Neotropical Mainland

The geographic range of mainland mormoopids extends from the northern limits of the Neotropics in North America (*Mormoops megalophylla* even extends slightly into the temperate regions of that continent) to near the southern limits of the Neotropics (Mato Grosso, Brasil) in South America. Generally the ranges of mainland species overlap broadly, with the exception of *Pteronotus suapurensis*, which has a somewhat restricted geographic range from southern México to as far south as Tingo María, Perú, and possibly the Mato Grosso region of Brasil. The center of origin from which the family dispersed is obscured by the absence of a fossil record. Origin of the group, however, could have been in southern Middle America or northern South America, areas that fall approximately in the middle of the present distribution of the mainland species of the family.

From the analyses of geographic variation, there is an indication that populations of *Pteronotus parnellii, personatus, davyi,* and *Mormoops megalophylla* have been split into northern and southern segments sometime in the past, leading to subspeciation. In *Mormoops*, there still remains a sizable gap between the two segments, which may in fact signal incipient species; without conclusive evidence, however, I treat the two as subspecies groups. The few specimens of *P. personatus* and *davyi* from Middle America suggest that the ranges of both are continuous, or nearly so, from North America into South America; certainly the range of *P. parnellii* is continuous.

In North America, the Mexican Plateau seems to be an important physical and ecological barrier to dispersal of members of the genus *Pteronotus*. The ranges of *P. parnellii, personatus,* and *davyi* extend northward along either side of the plateau into the lowlands of eastern and western México to the extreme northern limits of the Neotropics in the southern parts of Sonora and Tamaulipas. The tropical environment in western México (northern Sinaloa

and Sonora) is more arid than in eastern México. Specimens of *P. davyi fulvus* from Sonora are noticeably larger and exhibit more secondary sexual variation than do bats of most other Mexican populations of this subspecies. By comparison, specimens of *P. parnellii* from western México average smaller than bats of other mainland populations and exhibit little secondary sexual variation.

The Mexican Plateau has not been a barrier to the dispersal of *Mormoops megalophylla*, which is known from a number of localities on the plateau (Fig. 39). This species has been reported from as far north as southern Texas (including parts of the Edwards Plateau) and southern Arizona, and it is the only mormoopid presently known from Baja California. The exact nature of limiting factors to the distribution of this species are not yet well understood. Generally speaking, individuals of *M. megalophylla* are relatively small in México and northern Middle America, although there is considerable variation between populations. In Honduras and El Salvador, members of this species are slightly larger than bats from more northern localities.

The Isthmus of Tehuantepec, a lowland area in southern México over which a water barrier prevailed during periods of high sea level in the past, apparently has been of little consequence to the dispersal and speciation of mormoopid species excepting *P. parnellii*. *Pteronotus p. mexicanus*, a small and pale subspecies, apparently differentiated to the north of the isthmus, whereas the comparatively larger and darker *P. p. mesoamericanus* evidently differentiated in nuclear Middle America. Apparently gene flow between these two geographic units is less pronounced along the dry southern part of the isthmus than along the humid northern side. It is also interesting to note that the northernmost known occurrence of *P. suapurensis*, perhaps the most mesophyllic of the mormoopid species, is from San Andrés Tuxtla, Veracruz, which is situated about half way across the humid northern part of the isthmus.

Davis (1968, 1969) suggested that the ecological and physiographic conditions of the Caribbean and Pacific versants of Middle America have been important factors in the differentiation of subspecies in *Uroderma bilobatum* and *Artibeus phaeotis*. Unfortunately, there is a scarcity of material of most mormoopid species from critical areas in Middle America and an accurate appraisal of the effectiveness of these versants with reference to this group is not yet feasible. They do seem to have affected subspeciation in at least one species, *P. parnellii*. Populations assigned herein to *P. p. rubiginosus* and *P. p. mesoamericanus* are segregated along the humid Caribbean versant and semi-arid Pacific versant, respectively. These two subspecies are most distinct from each other in northern Nicaragua, probably owing to the rather broad ecotonal belt between the two versants in that area. Farther to the south, the versants come into closer proximity and the ecotonal belt is correspondingly narrower. In this region, *rubiginosus*-like bats dominate the zone of intergradation.

During the Pleistocene, the region of eastern Panamá and northwestern Colombia may have been of considerable importance to dispersal, both southward and northward, of *P. parnellii* as well as other mormoopids. Climatic fluctuations, which no doubt greatly influenced the extent of humid tropical forest throughout the Neotropics, probably resulted in changes in the character of the habitat in this narrow corridor. There likely was continuous arid habitat between the Caribbean coast of South America and Pacific versant of Middle America in dry epochs, whereas wet periods would have been conducive to continuous humid forest from the Amazon Basin through the Caribbean versant of Middle America.

In South America, considerably less

is known about the distribution of mormoopids and the features that influenced these patterns appear to be much more complex than in North America. As noted above, all five mainland species occur in South America. With the exception of *P. suapurensis*, all are represented there by populations that are subspecifically distinct from those of North America (although some, such as *Pteronotus parnellii rubiginosus*, *Pteronotus personatus personatus*, and *Pteronotus davyi davyi* extend northward into southern Central America). In three species (*P. parnellii*, *P. davyi*, and *M. megalophylla*) there are at least two recognizable South American subspecies.

Haffer (1967a, 1967b, 1969, 1970) examined the "nonforest" and "forest" bird faunas of northwestern South America and the Amazon Basin and has presented some interesting ideas concerning Pleistocene and post-Pleistocene zoogeography of that region. His arguments primarily revolve around forest expansion and contraction as a result of wet glacial periods and dry interglacial periods, and the corridors of dispersal that opened or closed with these fluctuations. Haffer's concepts can be applied easily to the bat fauna of this region.

During forest expansion in the Amazonian region, northward and southward dispersal of semi-xerophyllic species along the eastern slope of the Andes would have been effectively blocked, whereas in drier periods an arid corridor would have extended from northern Colombia and Venezuela along the eastern slope of the Andes to southern Brasil. Perhaps such a corridor permitted *Pteronotus davyi* to enter the Río Marañón Valley through which these bats spread and eventually crossed the Andes in the upper Huancabamba Valley to northwestern Perú (where the subspecies *P. d. incae* later differentiated).

Perhaps the most interesting area in South America is the region in northwestern Colombia through which north and south immigrants passed enroute to (or from) South America. This region is complicated by the position of the Colombian Andes and the dry intermontane Cauca and Magdalena valleys. Based on the presently known distributional patterns, the general pattern of mormoopid dispersal through this region apparently has followed along the Caribbean coast of Colombia and Venezuela. *Pteronotus parnellii*, *suapurensis*, and possibly *davyi* likely made their way to the Amazon Basin either over a depression in the Andes in western Venezuela or conceivably through the Delta Amacuro in eastern Venezuela.

Some populations of *Mormoops megalophylla* evidently migrated up the dry intermontane Cauca Valley and eventually into the upper Patía Valley on the dry Pacific versant of Ecuador, after having crossed the relatively low Andean pass that separates the two valleys. Subsequent isolation apparently resulted in the establishment of the distinctive subspecies *M. m. carteri* in this region. Both *M. m. carteri* and *P. d. incae* (discussed above) conceivably could have arrived in the arid Pacific region of Ecuador and Perú by dispersing along the narrow Pacific lowland corridor of western Colombia and Ecuador. Much of this region, however, is covered by humid tropical forest that probably developed in the early part of the Pleistocene according to Haffer (1967a) and Chapman (1926). This forest presumably would have blocked these two species because neither seems to be a deep forest inhabitant and it is doubtful that either arrived in western Ecuador and Perú before the Pleistocene, judging by the degree of morphological differentiation from other South American populations.

Mormoops megalophylla apparently is the only mormoopid that has successfully colonized the Dutch West Indies. Analysis of geographic variation indi-

cates that these insular populations have indeed differentiated subspecifically from those on the mainland, as was previously supposed. A certain amount of intergradation appears to be maintained through the continental island of Aruba, which is situated between the mainland and the islands of Curaçao and Bonaire.

It is interesting to note that *P. davyi* (a species known from the adjacent mainland and reported from as far north in the Lesser Antilles as Marie Galante) is apparently absent from the Dutch West Indian fauna, emphasizing the importance of niche availability as well as the fortuitous nature of insular invasion.

SUMMARY

The taxonomic history of the family Mormoopidae Saussure, 1860 is reviewed beginning with the description of *Mormoops* and *Aello* by Leach (1821). Most of the remaining taxa were discovered and described during the last half of the nineteenth century and have been allied with the families Noctilionidae and Phyllostomatidae. The correct derivation and authorship of the family-group name is documented.

Prior to this study, the mormoopid genera were arranged together in the subfamily Chilonycterinae (family Phyllostomatidae). This arrangement was tested utilizing evidence derived from a comparative examination of the osteological structure of distal and proximal ends of the humerus, proximal end of the femur, and structure of the tragus. These data are correlated with published results of other comparative studies involving acoustic orientation, hair structure, karyotypes, histological aspects of facial glands, ectoparasites, brain size, and immunologic studies. It is concluded that mormoopids comprise a family distinct from the Phyllostomatidae, both morphologically and behaviorally.

Owing to the absence of a substantial fossil record for bats, the phylogenetic relationships of the Mormoopidae are not readily apparent. Features of the external and internal anatomy seem to indicate that mormoopids likely are most closely related to the Noctilionidae and Phyllostomatidae, perhaps more closely allied with the former than the latter. It is postulated that all three of these families may have arisen as autochthonous lineages from a paleochiropteran stock present in the New World as early as middle to late Paleocene times.

Two genera, *Pteronotus* and *Mormoops*, are recognized; the former is divided into three subgenera, *Phyllodia*, *Chilonycteris*, and *Pteronotus*. Members of the genus *Mormoops* are more specialized than those of the genus *Pteronotus*; the dichotomy is marked by a number of unique features. Within *Pteronotus*, the subgenus *Phyllodia* is more distinct from *Chilonycteris* and *Pteronotus* than are the latter subgenera from each other.

Patterns of non-geographic variation (secondary sexual variation, individual variation, and seasonal variation with reference to pelage and molt) are discussed, and a key to the genera and subgenera is presented.

Patterns of geographic variation of each mormoopid species was statistically analyzed and correlated with the ecological and physiographic features of the regions inhabited by these species. Two species were found to be monotypic, whereas six are polytypic involving 21 subspecies, three of which *(Pteronotus parnellii mesoamericanus, Pteronotus davyi incae,* and *Mormoops megalophylla carteri)* are described as new.

The zoogeography of the family is obscured by the absence of a fossil record and extensive, broadly sympatric geographic distributions in the Neotropics. The center of origin of mormo-

opids could have been in southern Middle America or northwestern South America. Representatives of both genera have successfully invaded the Greater Antilles, presumably from the Middle American region, and have differentiated as full species or subspecies from their mainland relatives. Zoogeographic features that may have governed the dispersal and speciation, both on the Greater Antilles and the Neotropical mainland, are discussed.

RESUMEN

Se traza la história taxonómica de la familia Mormoopidae Saussure, 1860, partiendo de la descripción de *Mormoops* y *Aello* dada por Leach (1821). La mayoría de las especies de esta familia fue descubierta y descrita durante la segunda mitad del siglo 19 y ha sido intercolada entre las familias Noctilionidae y Phyllostomatidae. La derivación y la paternidad de autor del nombre de la familia son documentadas.

Anterior a esta investigación fueron colocados los géneros mormoopidos juntos en la subfamilia Chilonyeterinae (Familia: Phyllostomatidae). Esta colocación fue comprobada utilizando la evidencia obtenida de una examinación comparada de la estructura osteológica de las partes próximas y distales del húmero, de la parte próxima del fémur y la estructura del trago. Estos datos se correlacionen con resultados publicados en otros estudios comparados de ecolocación, la estructura del pelo, cromosomas, aspectos histológicos de glándulas faciales, ectoparasitos, tamaño del cerebro y estudios immunológicos. De ahí que los mormoopidos forman una familia distinta y separada de la Phyllostomatidae, tanto en cuanto a la morfología como en cuanto a la comportamiento.

Las relaciones filogenéticas de la Mormoopidae son borrosas debido a la ausencia de una buena historia fosilífera de los murciélagos. Según varias características de la morfología, parece que los mormoopidos tienen parentesco con las familias Noctilionidae y Phyllostomatidae, quizá más con la primera que con la segunda. Se sugiere que las tres familias, arriba mencionadas, se han evolucionado como líneas autóctonas de paleoquirópteros presentes en el Nuevo Mundo desde un momento tan temprano como el medio del Paleoceno.

Se reconocen dos géneros, *Pteronotus* y *Mormoops*. Se divide el género *Pteronotus* en tres subgéneros, *Phyllodia*, *Chilonycteris* y *Pteronotus*. La dicotomía entre los dos géneros es bien marcado por varios rasgos únicos. Dentro del género *Pteronotus*, la semejanza entre los dos subgéneros *Chilonycteris* y *Pteronotus* es mayor de lo que es la de cualquiera de los dos referente al *Phyllodia*.

Se comentan los patrones de variación sexual secundaria, individual y estacional con referencia al pelage y la muda. También, se presenta una clave referente a los géneros y subgéneros.

La variación geográfica de cada especie mormoopida fue analizada estadísticamente ye se comenta junta con los factores ecológicos y fisiográficos de las regiones en las que viven estas especies. Dos especies son monotípicas. Seis son politípicas y se traten de 21 subespecies. Se llaman a la atención tres de estas subespecies (*Pteronotus parnellii mesoamericanus*, *Pteronotus davyi incae* y *Mormoops megalophylla carteri*), las cuales son enteramente nuevas.

La zoogeografía de la familia también resulta borrosa no sólo por la ausencia de una historia fosilífera sino también por las distribuciones geográficas muy simpátricas en la Neotrópica. El centro de orígen se situada probablemente en el sur de la América Central o en las partes del noroeste de la América del Sur. Representantes de ambos

géneros florecen en las Antillas Mayores. Parece que estos murciélagos emigraron de la América Central y se han diferenciado en especies o subespecies de los parentes del continente. Se comentan los factores zoogeográficos que han influido en la dispersión y la evolución de la familia en las islas y el continente.

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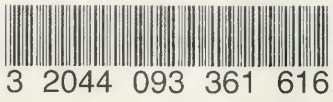
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